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A revision of the cladoceran genus *Simocephalus* (Crustacea, Daphniidae)

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CONTENTS

Introduction	2
Material and methods	3
Morphology	3
Variability	5
Systematic Accounts	6
Subgenus <i>Simocephalus</i> s. str.	6
<i>S. vetulus</i> (O.F. Müller, 1776)	7
<i>S. mixtus</i> Sars, 1903	11
<i>S. vetuloides</i> Sars, 1898	12
<i>S. punctatus</i> sp. nov.	14
<i>S. gibbosus</i> Sars, 1896	15
<i>S. elizabethae</i> (King, 1853)	16
Subgenus <i>S. (Echinocaudus)</i> subgen. nov.	20
<i>S. obtusatus</i> (Thomson, 1878)	21
<i>S. daphnoides</i> Herrick, 1883	21
<i>S. (exspinosus)</i> species group	22
<i>S. exspinosus</i> (De Geer, 1778)	22
<i>S. congener</i> (Koch, 1841)	25
<i>S. (acutirostratus)</i> species group	26
<i>S. acutirostratus</i> (King, 1853)	26
<i>S. victoriensis</i> Dumont, 1983	30
<i>S. brehmi</i> Gauthier, 1939	31
<i>S. rostratus</i> Herrick, 1884	31
Subgenus <i>S. (Coronocephalus)</i> Orlova-Bienkowskaja, 1995	39
<i>S. serrulatus</i> (Koch, 1841)	41
<i>S. semiserratus</i> Sars, 1901	46
<i>S. mirabilis</i> sp. nov.	49
Subgenus <i>S. (Aquipiculus)</i> Orlova-Bienkowskaja, 1995	52
<i>S. latirostris</i> Stingelin, 1906	53
<i>S. heilongjiangensis</i> Shi, Shi, 1994	53
<i>S. lusaticus</i> Herr, 1917	53
<i>Nomina dubia</i> and species transferred to the genus <i>Daphnia</i>	54
Key to the subgenera and species of <i>Simocephalus</i>	54
Check list of <i>Simocephalus</i>	60
Acknowledgements	60
References	60

SYNOPSIS. *Simocephalus*, a world-wide genus of littoral freshwater Daphniidae is reviewed in full for the first time. Four subgenera are recognized, one subgenus and two species are newly described. Eight species and subspecies are synonymized, a number of previously synonymized species are reinstated and two species are transferred to the genus *Daphnia*. Thus, twenty species are considered as valid members of the genus *Simocephalus*: subgenus *Simocephalus* s. str.: *S. vetulus*, *S. elizabethae*, *S. gibbosus*, *S. vetuloides*, *S. mixtus* and *S. punctatus* sp. nov.; subgenus *S. (Coronocephalus)*: *S. serrulatus*, *S. semiserratus* and *S. mirabilis* sp. nov.; subgenus *S. (Aquipiculus)*: *S. latirostris*, *S. lusaticus* and *S. heilongjiangensis*; new subgenus *S. (Echinocaudus)*: *S. exspinosus*, *S. congener*, *S. acutirostratus*, *S. obtusatus*, *S. daphnoides*, *S. rostratus*, *S. brehmi*, *S. victoriensis*. For each species, accounts are given of nomenclature, distribution and morphology (with original figures). A key for identification of subgenera and species is provided.

INTRODUCTION

Freshwater Daphniidae of the genus *Simocephalus* Schödler, 1858 are common in littoral aquatic vegetation all over the world. These 'tailless water fleas' have been known since the middle of the 18th century (Schaeffer, 1755), but their taxonomy remains unsettled, with 61 specific and subspecific names proposed. Morphological variability is poorly known. This makes the taxonomic status of certain forms doubtful, since they may not represent taxa, but merely morphological varieties. The descriptions of numerous species are inadequate. Furthermore, some species which are supposed

to be cosmopolitan, pantropical *etc.* are in fact groups of closely related species, with restricted distributions. Obviously, a world-wide revision of *Simocephalus* is necessary. Such an attempt is made here.

The genus *Simocephalus* has been divided into four species groups: *S. (vetulus)*, *S. (exspinosus)*, *S. (serrulatus)* and *S. (latirostris)* (Orlova-Bienkowskaja, 1993a). The diagnostic characters of the groups are stable and well-expressed in all representatives. Intermediate forms are absent. Furthermore, different characters are congruent, that is, they combine species into the same groups. Thus the species groups are given the rank of subgenera.

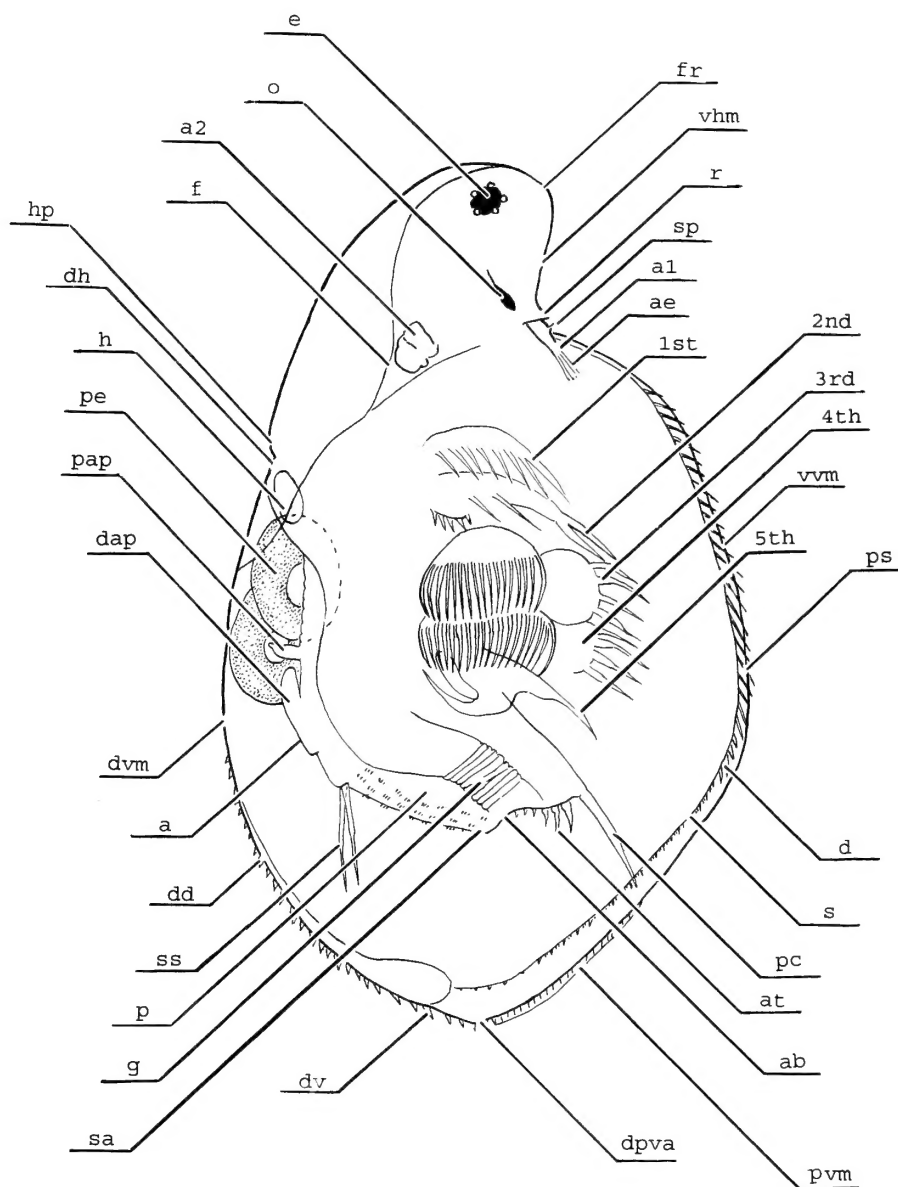


Fig. 1 Morphology of *Simocephalus*. a – abdomen, ab – anal bay, ae – aesthetes, at – anal teeth, a1 – antennule, a2 – base of antenna (antenna is not shown), d – denticles of inner surface of ventro-posterior valve angle, dap – distal abdominal process, dd – denticles of dorsal valve margin, dh – depression of head shield between head and valves, dpva – dorso-posterior valve angle, dv – point of divergence of valves, dvm – dorsal valve margin, e – eye, f – fornices, fr – frons, g – gut, h – heart, hp – the place of head pores, o – ocellus, p – postabdomen, pap – proximal abdominal process, pc – postabdominal claw, pe – parthenogenetic eggs, ps – plumose setae of inner surface of ventral valve margin, pvm – posterior valve margin, r – rostrum, s – setules of inner surface of posterior valve margin, sa – supra-anal angle, sp – sensory papilla of antennule, ss – sensory setae, vbm – ventral head margin, vvm – ventral valve margin, 1st – 1st trunk limb, 2nd – 2nd trunk limb, 3rd – 3rd trunk limb, 4th – 4th trunk limb, 5th – 5th trunk limb.

MATERIALS AND METHODS

About ten thousand specimens from more than three hundred localities all over the world have been studied. Females of all species except *S. lusaticus*, males of nine species, and museum types of fifteen taxa have been examined. Material examined is in the following collections and institutions: AC – author's collection deposited in Zoological Museum of Moscow State University, AM – Australian Museum, Sydney, Australia, BMNH – The Natural History Museum, London, Great Britain, MCA – Museum of Central Africa, Tervuren, Belgium, MNO – Museum of Nature, Olten, Switzerland, MV – Museum of Victoria, Australia, SAM – South Australian Museum, Adelaide, Australia, ZI – Zoological Institute of the Russian Academy of Sciences, St.-Petersburg, Russia, ZICC – Cladocera collection of ZI, ZICW – G.Ju. Werestchagin's collection in ZI, ZIPD – plankton depository of ZI, ZMC – Zoological Museum of Copenhagen, Denmark, ZMO – Zoological Museum of Oslo University, Norway, ZMU – Zoological Museum of Uppsala University, Sweden.

Original figures are made with the aid of a camera lucida. Keys and diagnoses are based on adult specimens. The following additional abbreviations are used: CBS – canadian balsam slide, MPA – material preserved in alcohol, PSEM – preparation for scanning electron microscopy, PVAS – polyvinyl alcohol slide, ♀ ad. – adult parthenogenetic female, ♀ juv. – juvenile parthenogenetic female, ♀ e. – ephippial female. Morphological terms used below are shown on Fig. 1.

In some cases I use a cluster analysis and diagrams of characters for differentiation between closely related species. Four metric characters are used (Fig. 2): W/L – ratio between width of dorso-posterior valve prominence and body length, M/L – ratio between length of dorso-posterior valve prominence and body length, G/L – ratio between height of dorsal valve margin and body length, D/L – ratio between diameter of dorso-posterior valve prominence and body length. Body length (L) was measured with an ocular micrometer. Other measurements were made by drawing the body outline of each specimen with the aid of the camera lucida and measuring the details with an ordinary rule.

Statistical analysis employed the computer system 'Statgraphics'. Two-dimensional diagrams of characters are used for the detection of morphological hiatus between closely related species. Each specimen of each series is represented as a point on a coordinate plane. Coordinates of the point are equal to measurements of the specimen. Each series or group of series is represented with the polygon including the points corresponding to all specimens. If the polygons of two series/ groups of series do not overlap, there is a

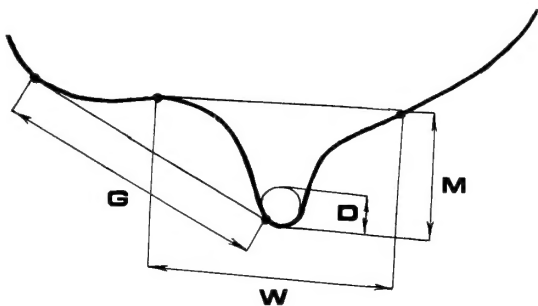


Fig. 2 Measurements of valves. G – height of dorsal valve margin, W – width of dorso-posterior valve angle, D – diameter of dorso-posterior valve angle, M – length of dorso-posterior valve angle.

morphological hiatus between them. I also use four-dimensional cluster analysis (average method) to determine which series are close to each other. Diagrams of characters and cluster analysis are independent of each other, because the former operates only with extreme values, the latter only with average values of characters. Therefore, if both methods give the same result, it is reliable.

MORPHOLOGY

Female

Valves

Maximum height of valves posterior to the middle. (Figs 1; 3B,C). Posterior margin (Fig. 1:pvm) oblique, almost straight. Point of divergence of valves (Fig. 1:dv) dorsal to dorso-posterior angle (Fig. 1:dpva). Dorsal, posterior and ventral margins with denticles or smooth. Denticles arranged in 2 rows on dorsal margin (Fig. 1:dd). Inner valve surface with a row of plumose setae on ventral margin (Fig. 1:ps), a row of setules groups on posterior margin (Fig. 1:s) and 2–5 plumose denticles near ventro-posterior angle (Fig. 1:d). Parthenogenetic female with 1–30 eggs in brood pouch. Ephippium containing 1 egg (Fig. 3C).

Reticulation

Valves and head reticulated. Reticulation consists of oblique stripes somewhat intersecting in most of carapace and head and of polygons along valve margin and in front of eye.

Head

Comparatively small, noticeably delimited by depression on dorsal side (Fig. 1:dh). Rostrum always pointed, long or moderate. Frons (Fig. 1:fr) rounded, pointed or right-angled, with denticles or devoid of them. Ventral head margin (Fig. 1:vhm) with depression, deep or shallow, near rostrum. Fornices very broad (Figs 4; 5; 1:f). Posterior part of head with 3 main connected head pores, transversally orientated (Fig. 5, HP) and 2 minute lateral head pores seen only with scanning electron microscope, or without head pores. Eye and ocellus always present.

Appendages

Antennule tubular (Figs 6C), having 9 aesthetes at end and 1 sensory papilla proximally. Mandibles, maxillule and labrum as shown in Figs 4, 6. Antenna (Fig. 7) comparatively short, ends of distal segments reach only middle of valves. Proximal part of basipod with 2 setae (Fig. 7E), outer side of distal part with a seta (Fig. 7D), inner side of distal part with a spine (Fig. 7C). Contrary to the opinion of Manujlova (1964), the length of the distal seta does not differ in different species. Exopod of antenna of 4; endopod of 3 cylindrical segments. Second segment of exopod with a short spine, third with a seta, fourth with 3 setae, of which one shorter than others and curved (Fig. 7B). First and second endopod segment each with 1 seta, third segment with 3 setae. Contrary to the opinion of Behning (1912) and Manujlova (1964) number of setae on each trunk limb does not differ in different species. Interspecific differences concern only the length of certain setae. The structure of trunk limbs (Figs 6; 8–11) has been described in detail (Orlova-Bienkowskaja, 1993b).

Postabdomen (Figs 1:p; 12A,B)

High, with anal bay (Fig. 1:ab), supra-anal angle (Fig. 1:sa) and 2 rows of anal teeth (Fig. 1:at). Distal anal teeth large, covered with setules. Proximal teeth small, smooth. Dorsal part with groups of

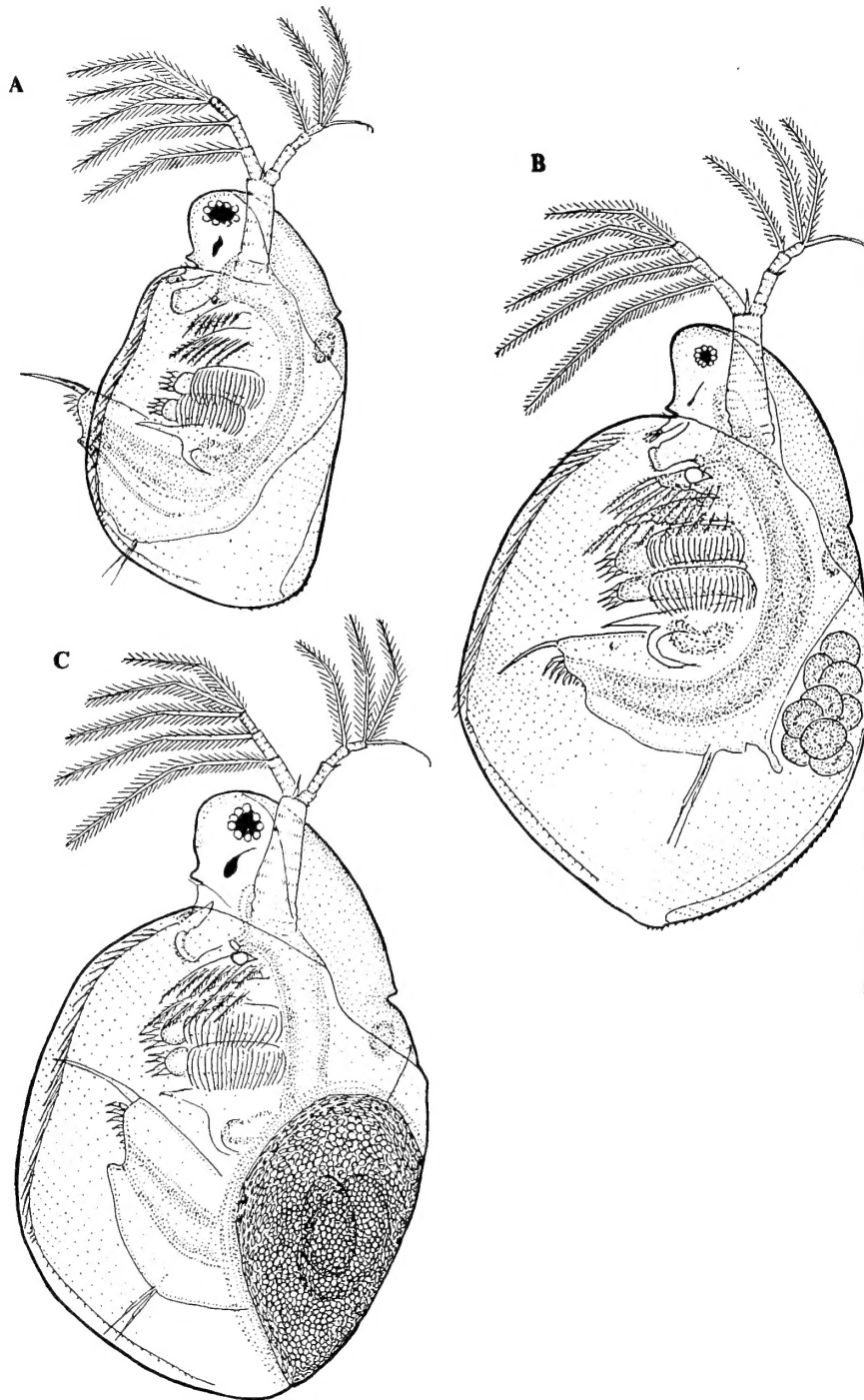


Fig. 3 *S. vetulus*. A, male, B, parthenogenetic female attached to a surface, C, ephippial female.

setules. Postabdominal claws long (Fig. 1:pc), slightly curved, with 2 rows of setules and/or spines on concave side. Anus (Fig. 1:ab) in anal bay.

Abdomen with 2 processes (Fig. 1:pap,dap).

Male

Dorsal valve margin straight (Fig. 3A), ventral margin with an embayment anteriorly. Head pores larger, antennules shorter and

more distended than in female (Fig. 6B), with 2 sensory papillae proximally. First and second trunk limbs (Figs 8B,C; 13) differ from corresponding limbs of female in several details (Orlova-Bienkowskaja, 1993b) (Figs 8A and C). Postabdomen narrower than in female (Fig. 14A). Vas deferens opening on supra-anal angle (Fig. 14B,C) or distally. Fewer anal teeth than in female.

Abdominal processes absent.

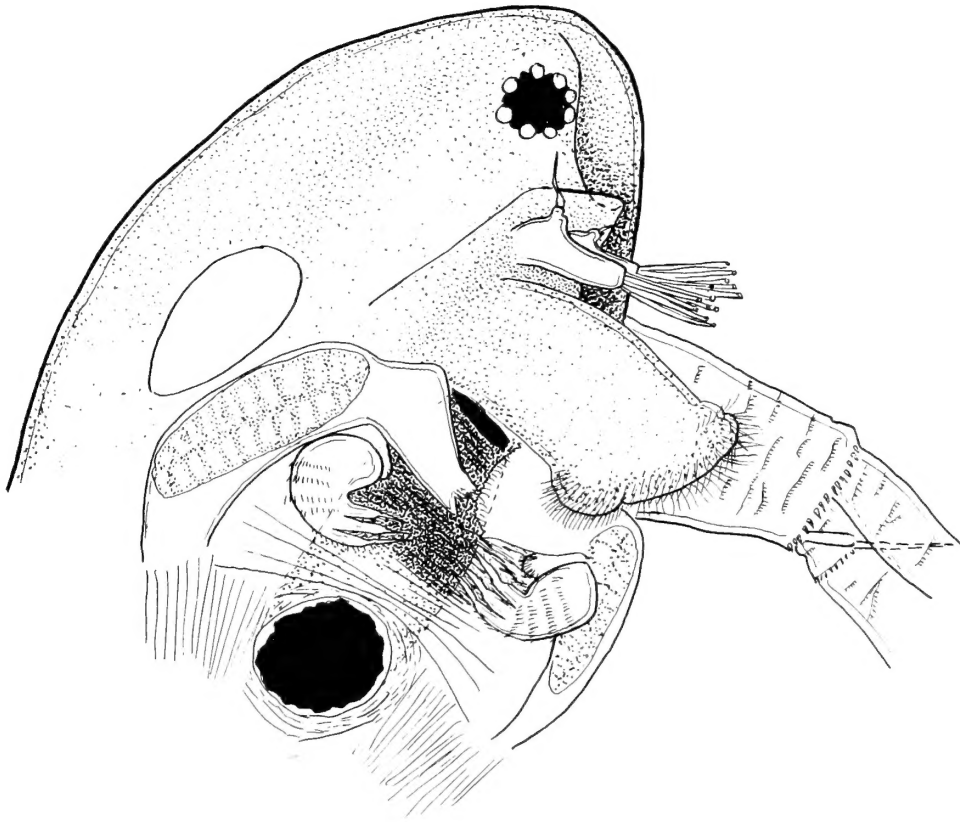


Fig. 4 *S. vetulus* head and mouth parts.

VARIABILITY

Age variability is similar in all species (Fig. 15). New-born females do not differ much from males: The brood pouch is small and the dorsal valve margin almost straight. The prominence on the dorso-posterior valve angle, if it present, is not distinct. Carapace denticles are small and cover less of the valves than in adults. Older females have a more distinct and sharp dorso-posterior valve prominence. The shape of the brood pouch in the adult depends on the number of eggs. The head grows slower than the carapace. Valve shape in new-born males differs from that of adults only in the absence of an embayment in the proximal part of the ventral margin. The number of anal teeth correlates with size in females. The ocellus in juveniles is shorter than in adults. The postabdomen of neonates of both sexes lacks an anal bay, supra-anal angle (Figs 12C; 15C), abdominal processes. The fourth endite prominence of the first limb has a large hook bearing a denticle at its end in the adult male (Fig. 8B) and small hook lacking a denticle in the juvenile (Fig. 8D). The curved setae of the second, third and fourth endite prominences of the second limb are short in juvenile males and longer than the base of the plumose seta of the first prominence in adults (Fig. 13B–D). The morphology of third, fourth and fifth trunk limbs in males and all trunk limbs in females does not depend on age.

Eye and ocellus size are subject to seasonal variation. This was discovered in the following way: two series of *S. vetulus* were collected in the same water-body in the Moscow region on 12. 5. 1990 and 5. 11. 1990. All specimens from the first sample had a

small eye and ocellus (Fig. 16A) and all those from the second (parthenogenetic and ephippial females and males) a large one (Fig. 16B). Individuals from the sample of 5. 11. 1990 were kept at room temperature. By the 17th day the size of the eye and ocellus in all cases had become small (Fig. 16C). A similar result was obtained for *S. serrulatus*.

Ocellus size is also affected by illumination intensity. It decreases in darkness (Jermakov, 1924) and if the ventral part of the head is covered by epibionts (personal observation) (Fig. 16D). Ocellus shape varies within populations. In females of *Simocephalus* s. str. it is straight or curved, widened in the middle or bifurcated at the end. In males of these species and in both sexes in species of other subgenera it is round or rhomb-like. The frons in *S. (Coronocephalus)* bears a variable number of denticles. Individuals with and without a prominence at the ventral head margin occur in all species except *S. gibbosus*, *S. elizabethae* and *S. obtusatus*. A dorsal embayment between carapace and head is more or less developed in all species. Sometimes, there is a small prominence on the head near this embayment (Fig. 16F).

There are pigmented spots in the valve tissue. Their shape and colour differ within populations. The colour is green, brown or orange and as a rule correlates with the colour of the gut contents. According to Green (1966) carotenoid pigmentation depends on the food composition.

The number of denticles at the ventro-posterior angle of the valves varies from two to six. No correlation between number of denticles and size was observed. There is some variability in shape of the postabdomen and abdominal processes (Fig. 17).

SYSTEMATIC ACCOUNTS

Subgenus *Simocephalus* s. str.

TYPE SPECIES. *Simocephalus vetulus* (O.F. Müller, 1776)

DIAGNOSIS. Both sexes. Frons rounded, without denticles (Fig. 18). Head shield without depression. Head pores present (Fig. 5). Insertion of antennules at base of rostrum. Antennule short in correspondence with short rostrum, with neither ridges nor denticles on inner side (Fig. 6B,C). Aesthetes longer than base of antennule. Postabdominal claws without spines (Fig. 12D,E). Inner and outer side of claw with fine setules. Anal bay of postabdomen narrow, rounded, with anal teeth (Fig. 12A).

Female. Dorso-posterior valve angle rounded or with rounded prominence. Valves without dorsal keel. Posterior corner of ephippium without protuberance (Fig. 3C). Ocellus elongate (exception: *S. punctatus*). Setae of 2nd and 3rd endite prominence of 2nd trunk limb as long as 0.3 and 0.2 of basal segment of plumose seta of 1st prominence respectively (Fig. 9B). Postabdomen with 10–15 anal teeth on each side. Supra-anal angle rounded (Fig. 12A). Male. Supra-anal angle pointed (Fig. 14). Vas deferens opening there. Postabdomen with 5–8 anal teeth on each side. Dorso-posterior valve angle rounded or with small rounded prominence (Fig. 3A). Males of the following species have been examined: *S. vetulus*, *S. mixtus*, *S. vetuloides*, *S. punctatus*, *S. elizabethae*. They do not differ from each other, so only females are described.

REMARKS. Fig. 19A gives the cluster analysis of sixteen series (each consisting of twenty specimens) from sixteen European

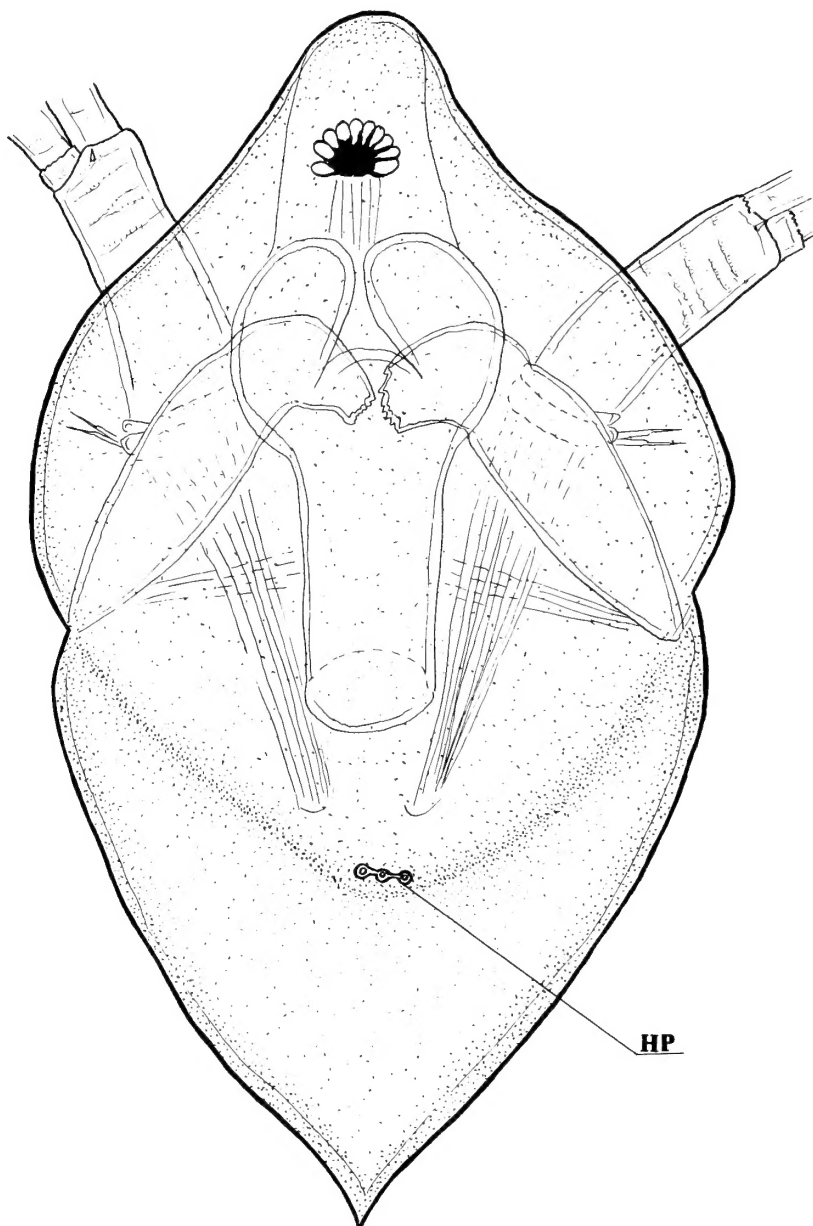


Fig. 5 *S. vetulus*. Head shield. HP – head pores.

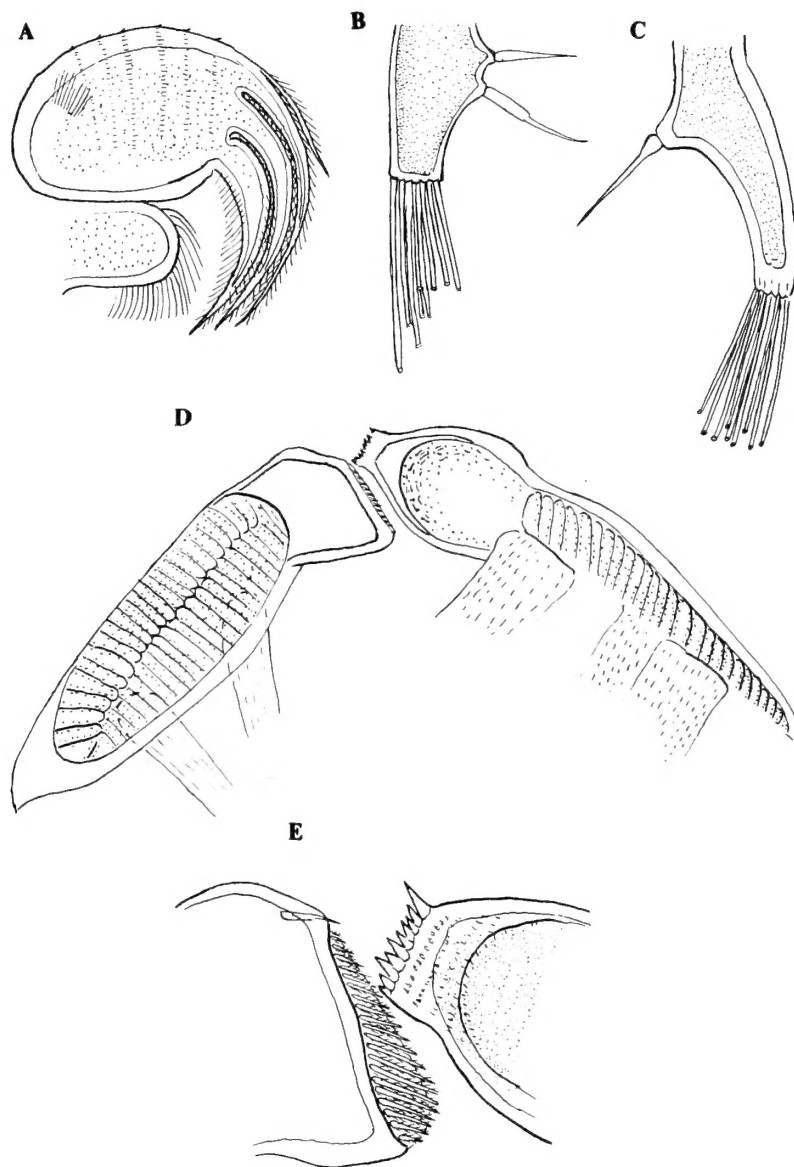


Fig. 6 *S. vetulus*. A, maxillule, B, antennule of male, C, antennule of female, D, mandibles, E, molar region of mandibles.

populations of *Simocephalus* s. str. The dendrogram consists of 2 large clusters. The first of them combines the populations 1–13 (thin line), and the second combines 14–16 (thick line). This means that the similarity within both clusters is stronger than between them. In other words, we can presume that populations 1–13 and 14–16 belong to two separate species. The diagrams of characters provide support for this presumption (Fig. 19B,C). The areas occupied by populations 1–13 (thin line) and by populations 14–16 (thick line) on the diagram only overlap to a minor extent at one point. Therefore, there is a morphological hiatus between these groups. Examination of the types shows that one of these species is *S. vetulus* (1–13); the other is *S. mixtus* (14–16).

Similar reasoning shows that 2 species of *Simocephalus* s. str.: *S. mixtus* and *S. vetuloides* occur in Eastern Siberia (Fig. 20). There appear to be 3 species in Eurasia: *S. vetulus* in Europe, *S. vetuloides* in Eastern Siberia and *S. mixtus* in all regions of Asia and in Eastern Europe. The latter species is rather variable.

All measured African specimens (9 series) belong to *S. mixtus*. I

have also one series of *S. vetulus* from Morocco, but these specimens are in poor condition and it is impossible to measure them.

S. vetulus (O.F. Müller, 1776)

Figs 3–18

Daphne vetula O.F. Müller, 1776: 199; *Daphnia sima* O.F. Müller, 1785: 91; *Monoculus nasutus* Jurine, 1820: 133; *Monoculus sima*: Jurine, 1820: 129; *Simocephalus vetulus*: Schödler, 1858: 18; *S. vetulus* var. *angustifrons* Lilljeborg, 1900: 171; *S. vetulus* var. *brandti* Cosmovici, 1900: 156 syn. nov. (nec *Daphnia brandtii* Fischer, 1848); *S. vetulus angustifrons*: Behning, 1941: 181; *S. vetulus gebhardti* Ponyi, 1955: 313; *S. mixtus hungaricus* Ponyi, 1956: 57.

TYPE MATERIAL. The types appear to be lost. *S. vetulus* is often confused with closely related species, so the designation of a neotype is necessary. Neotype (designated here): Denmark, Zealand, vicinity of Copenhagen. Dyrehaven, 55°46'N, 12°34'E, 11. 5. 1901: MPA: ♀ ad. (ZMC, CRU-319).

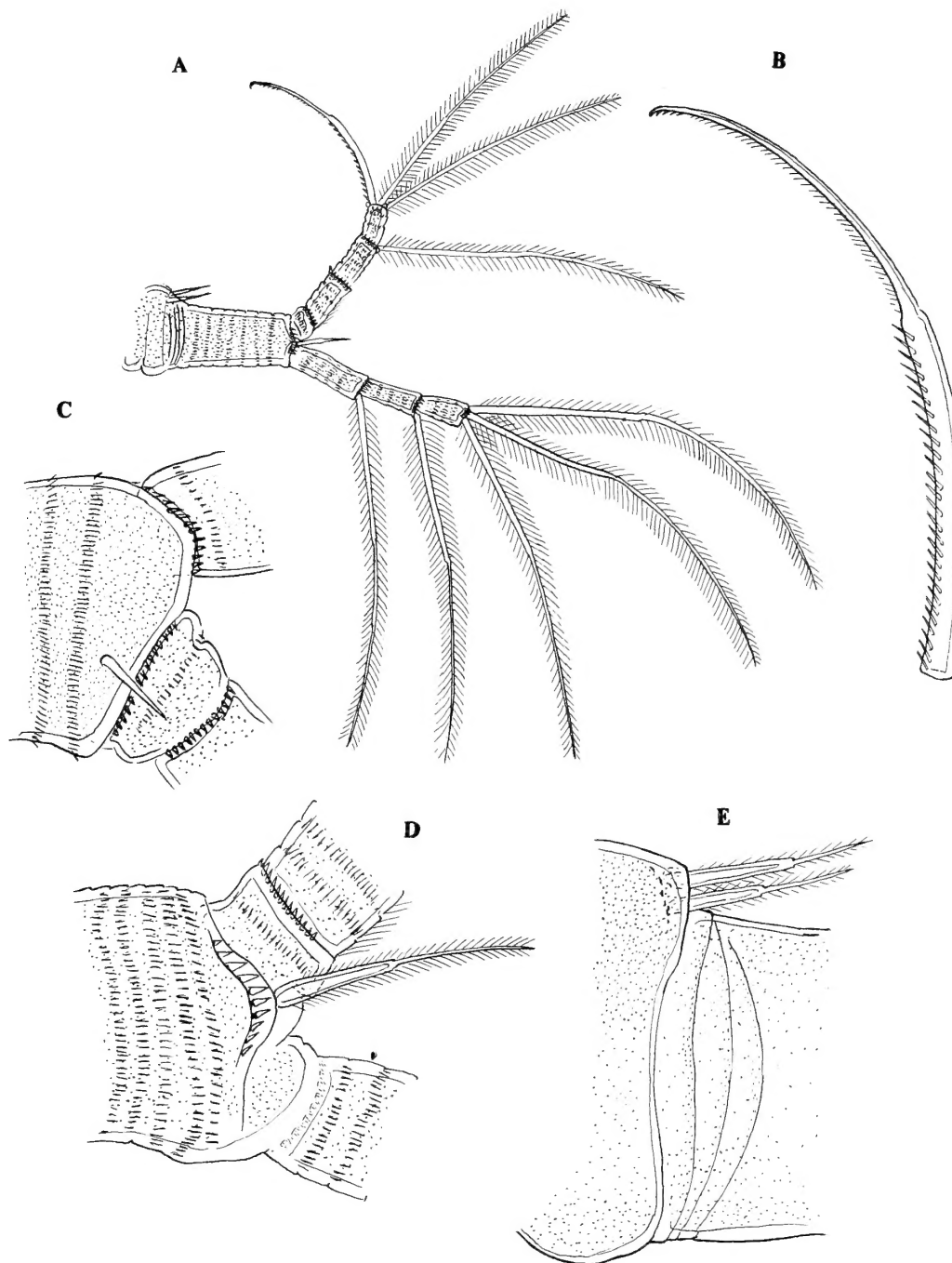


Fig. 7 *S. vetulus*, antenna. A, general view, B, curved seta of exopod distal segment, C, inner side of basipod, distal part, D, outer side of basipod, distal part, E, basipod proximal part.

MATERIAL EXAMINED. Neotype. Type material of junior synonyms: *S. vetulus angustifrons* Lilljeborg, 1900: Lectotype (designated here): Sweden, Uppsala, 9. 10. 1882, leg. Lilljeborg: MPA: ♀ ad. (ZMU, 399). Paralectotypes collected with lectotype: MPA: 13 ♀ ♀ ad., 33 ♀ ♀ juv., 7 ♀ ♀ e., 5 ♂ ♂ (ZMU, 399). Other specimens: More than 2000 specimens (♀ ♀ ad., ♀ ♀ juv., ♀ ♀ e., ♂ ♂) from 30 localities (Fig. 21) in Denmark, Greenland, Poland, Bulgaria, European Russia, Ukraine, Georgia, Morocco, deposited in AC, ZMC, ZICW. Some specimens are selected from the samples from ZIPD.

DIAGNOSIS. Measurements. ♀ ♀ ad.: 1.3–2.9mm., ♀ ♀ e.: 1.2–1.9mm, ♂ ♂: 1.1–1.3mm.

Female. Dorso-posterior valve prominence short, with narrow base and large diameter (Fig. 18). Its diameter greatly exceeds its length (Fig. 2). Dorsal valve margin low, not protruding backward. Depressions above and below dorso-posterior prominence small and shallow. Ventral head margin straight or slightly concave, sometimes with small prominence. Deep depression on ventral head margin near rostrum. Ocellus elongate.

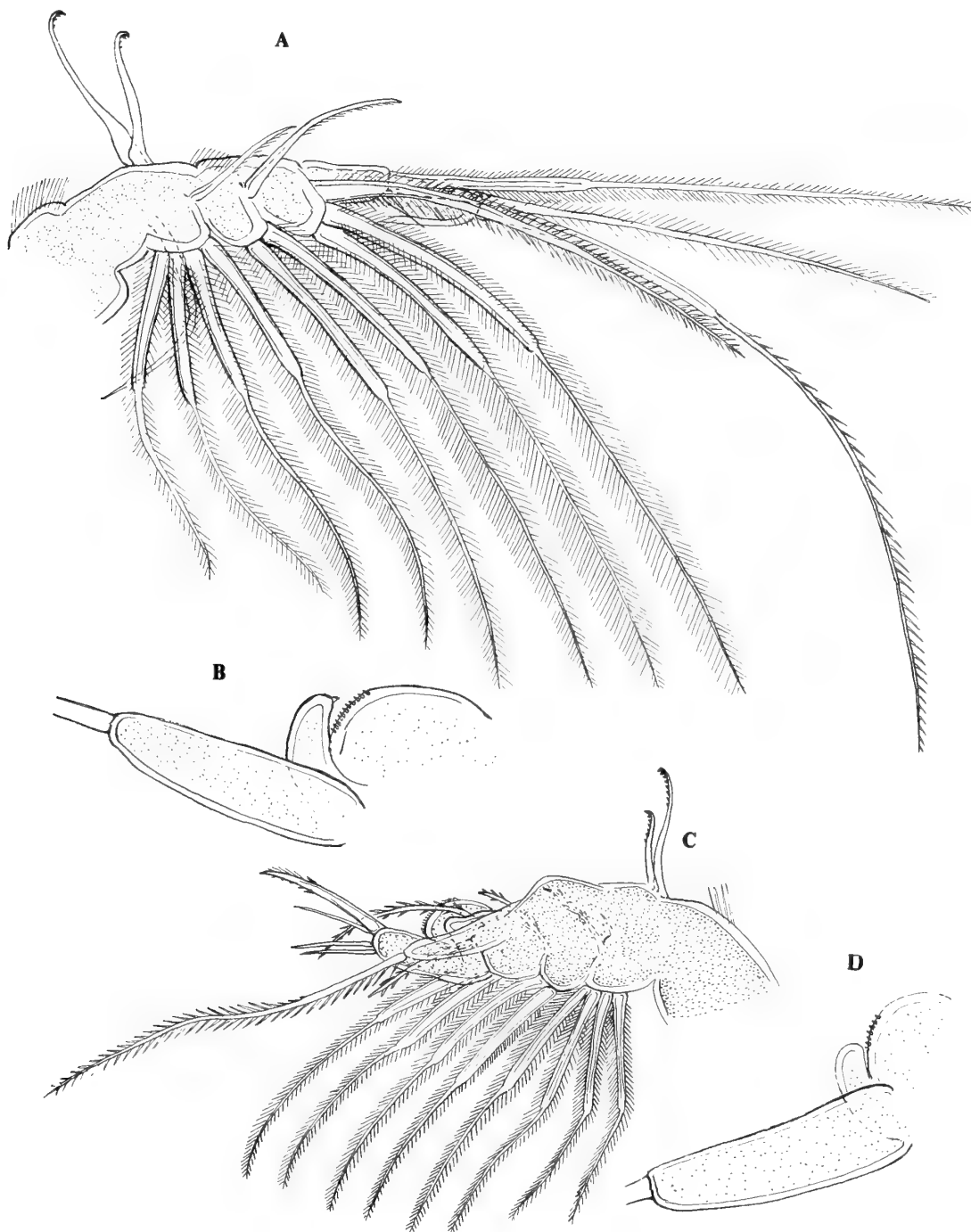


Fig. 8 *S. vetulus*. A, 1st limb of female, B, hook of endopod of 1st limb of adult male, C, 1st limb of male, D, hook of endopod of 1st limb of juvenile male.

DISTRIBUTION. (Fig. 21) Europe, North Africa. This species was previously assumed to be cosmopolitan (Manujlova, 1964). But the investigation of specimens from different regions shows, that *S. vetulus* occurs in Europe and North Africa only. In other regions it is replaced by closely related species: *S. mixtus*, *S. vetuloides*, *S. gibbosus*, *S. elizabethae* and *S. punctatus*.

REMARKS. The original description of *S. vetulus* is very short: 'Daphne Vetula cauda inflexa, testa mutica' (Müller, 1776). This is appropriate for any species of *Simocephalus*. Later, Müller (1785)

renamed this species *Daphnia sima*. The name 'vetulus' is not grammatically correct (Dumont, 1977). 'Vetula' means 'an old woman'. This is not an adjective, but a substantive. Its gender cannot alter. However, it is not necessary to change the name '*S. vetulus*', because it has come into common use.

Some authors in the 19th century (Lievin, 1848; Baird, 1850; Leydig, 1860) supposed *S. exspinosus* and *S. congener* to be synonyms of *S. vetulus*. According to recent data, *S. vetulus* differs very much from these species and even belongs to another subgenus.

According to Jurine (1820), *S. nasutus* (*Monoculus nasutus*

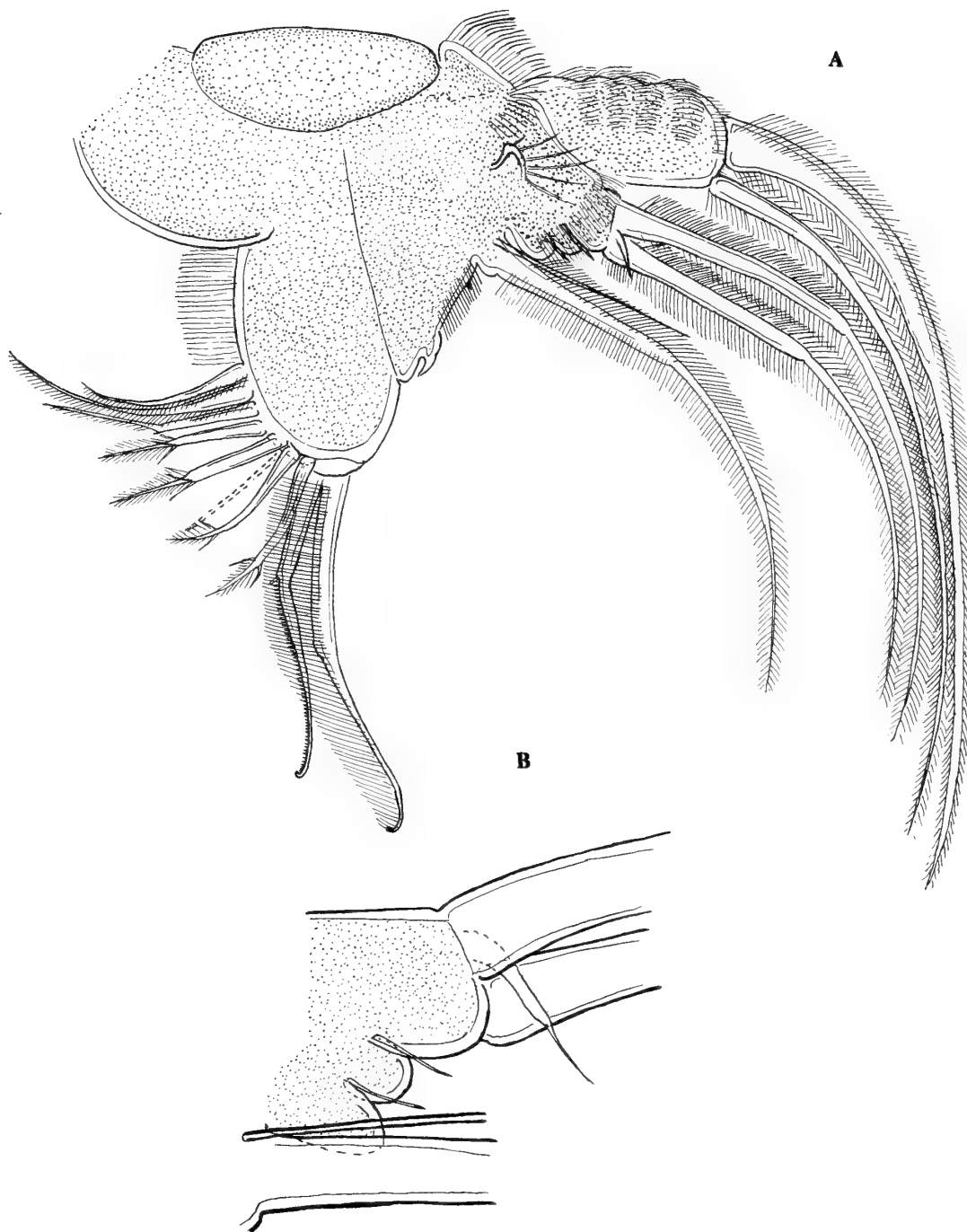


Fig. 9 *S. vetulus*, female 2nd trunk limb. A, general view, B, endopod.

differs from *S. vetulus* (*Monoculus sima*) in rostrum shape. However, judging from the illustrations in the original description, these species are identical. Information about the types of *S. nasutus* is lacking. I agree with Lilljeborg (1900), that *S. nasutus* is a junior synonym of *S. vetulus*.

S. vetulus var. *brandtii* Cosmovici was described from Romania. There is no information about the type material. Cosmovici (1900) writes that he named this variety thus because it is intermediate between *S. vetulus* and *S. brandtii* Fischer (= *S. serrulatus*). Referring to the illustrations by Cosmovici, it is the junior synonym of *S. vetulus*.

S. vetulus var. *angustifrons* Lilljeborg differs from the typical form in the presence of a prominence on the ventral head margin. Some authors (Behning, 1941; Manujlova, 1964) consider this variety to be a subspecies, but I believe it to be a synonym, because I have found specimens both with and without the prominence in the type material of *S. vetulus* var. *angustifrons* (Fig. 22). Moreover the animals with such a prominence sometimes occur in the most of *Simocephalus* species.

S. vetulus gebhardti and *S. mixtus hungaricus* were described from Hungary. The author (Ponyi, 1955, 1956) writes that these subspecies differ from *S. vetulus vetulus* in head shape and denticles

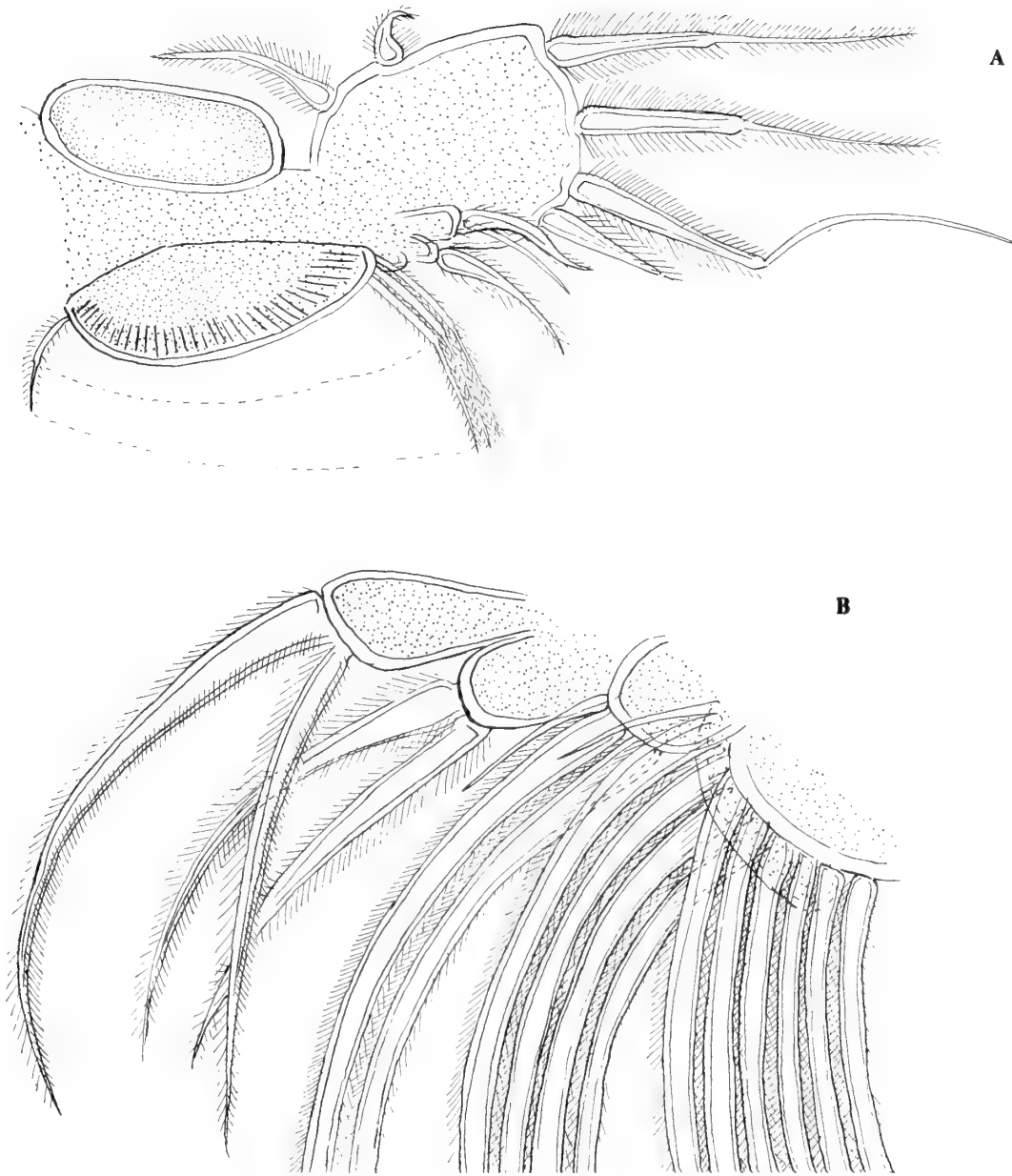


Fig. 10 *S. vetulus*, female 3rd trunk limb. A, general view, B, endopod.

on the dorsal margin of valves. However, judging from illustrations, *S. vetulus gebhardti* and *S. mixtus hungaricus* are identical to *S. vetulus vetulus*. The type material was destroyed during the battle in Budapest in 1956 (Ponyi, personal communication). I agree with Negrea (1983), that both names are the junior synonyms of *S. vetulus*.

S. mixtus Sars, 1903

Fig. 23

Simocephalus mixtus Sars, 1903: 174; *S. corniger* Methuen, 1910: 158 syn. nov.; *S. elizabethae*: Manujlova, 1964: 148, partim; *S. vetulus*: Flössner, 1986: 179, partim. *S. beianensis* Shi, Shi, 1994: 405 syn. nov.

TYPE MATERIAL. Lectotype (designated here): Mongolia, Eastern slope of Khingan mountain, 8. 11. 1911: MPA: ♀ ad. (BMNH, 1995.742). Paralectotypes collected with lectotype: MPA: 14 ♀ ad., 16 ♀ juv. (BMNH, 1995.743–752).

MATERIAL EXAMINED. Lectotype, paralectotypes and other specimens: more than 2500 specimens (♀ ad., ♀ juv., ♀ e., ♂) from 58 localities (Fig. 21) in Russia, Azerbaijan, Uzbekistan, Tadjikistan, Kirgizia, Kazakhstan, Mongolia, China, Sri-Lanka, India, Pakistan, Bangladesh, Vietnam, Azores, Algeria, Sudan, Egypt, Ethiopia, USA, Jamaica. Material is deposited in AC, ZICW. Some specimens are selected from the samples in ZIPD.

DIAGNOSIS. Measurements. ♀ ad.: 1.0–2.9mm, ♀ e.: 1.2–1.9mm, ♂: 1.0–1.3mm.

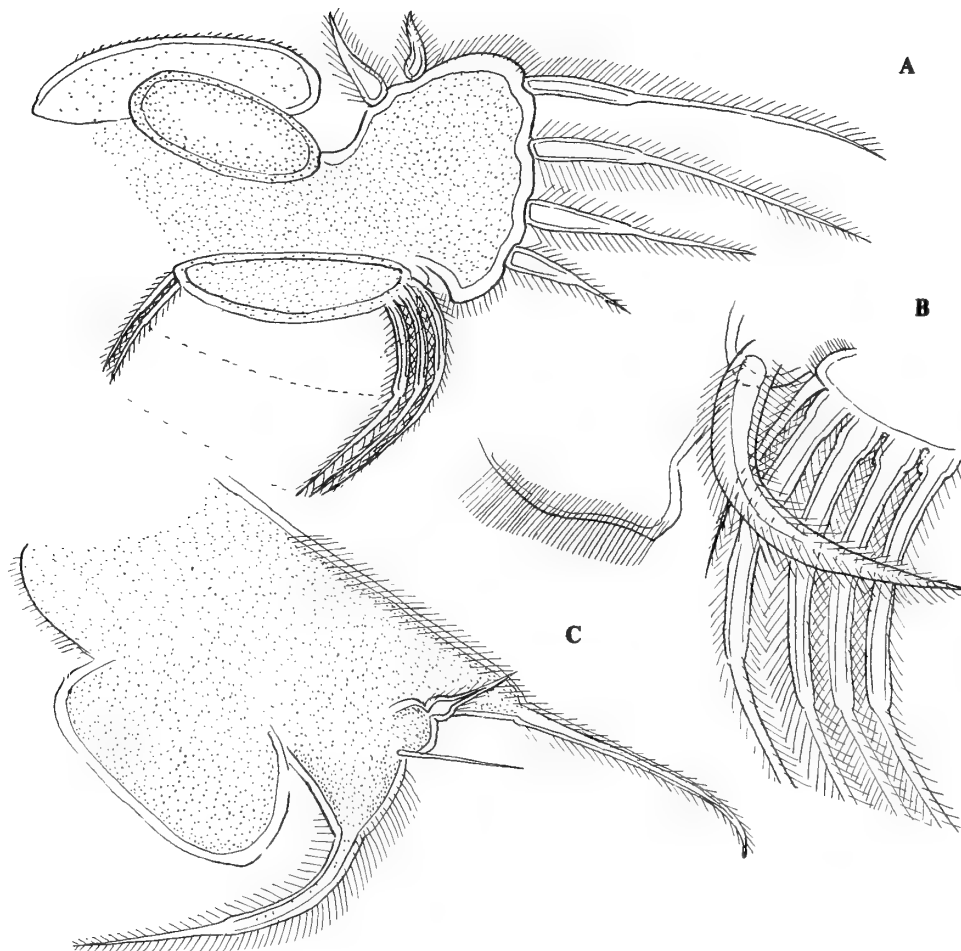


Fig. 11 *S. vetulus*, female trunk limbs. A, 4th limb, B, endopod of 4th limb, C, 5th limb.

Female. Dorso-posterior valve prominence of moderate length, with wide base and large diameter (Fig. 23). Its diameter (Fig. 2) exceeds its length. Dorsal valve margin high, protruding backward. Depressions above and below dorso-posterior prominence of moderate size (deeper than in *S. vetulus*, but more shallow than in *S. vetuloides*, *S. gibbosus* and *S. elizabethae*). Ventral head margin straight or slightly concave, sometimes with small prominence. Depression on ventral head margin near rostrum deep. Ocellus elongate.

DISTRIBUTION. (Fig. 21) Asia, Eastern Europe, N. Africa, N. America.

REMARKS. Behning (1941) supposes *S. mixtus* to be a separate species. Manujlova (1964) believes it to be a synonym of *S. elizabethae*. Negrea (1983) and Flössner (1972) consider it to be a synonym of *S. vetulus*. Investigation of the type has shown that *S. mixtus* differs from both *S. vetulus* and *S. elizabethae*.

S. corniger Methuen was described from South Africa. There is no information about the type material. The original description (Methuen, 1910) is very brief. Judging from illustrations, *S. corniger* is a junior synonym of *S. mixtus*.

S. beianensis Shi, Shi, 1994 was described from China (Heilongjiang Province, 48°16'N, 126°31'E) (Shi & Shi, 1994). The authors write that this species differs from *S. vetulus* in details of ocellus and in number of the anal teeth. Both characters are variable.

Referring to the illustration, the ocellus of *S. beianensis* does not sufficiently differ from the ocellus of *S. vetulus* and *S. mixtus*. The number of anal teeth does not also differentiate these species.

S. mixtus hungaricus Ponyi, 1956 is not in fact *S. mixtus*. It is a synonym of *S. vetulus* (see above). *S. serrulatus* var. *mixta* Grochmalicki (1915) belongs to another subgenus. It is a junior homonym of *S. mixtus*.

S. vetuloides Sars, 1898

Fig. 24

Simocephalus vetuloides Sars, 1898: 328; *S. elizabethae*: Behning, 1941: 182 partim; Manujlova, 1964: 148; *S. vetulus*: Fryer, 1957: 225 partim; Negrea, 1983: 138 partim.

TYPE MATERIAL. Lectotype (designated here): Russia, North Siberia, Jana river, 30. 6. 1885, leg. Ignatov: MPA: ♀ ad. (ZICC, 4690). Paralectotypes collected with lectotype: 38 ♀ ♀ ad. (ZICC, 4690). The vicinity of Jana river: CBS: ♀ ad. (ZICW). Dolgulach, 16–18. 6. 1885: 3 ♀ ♀ ad. (ZICW).

MATERIAL EXAMINED (Fig. 21). Lectotype, paralectotypes and other specimens from AC: Russia, vicinity of Yakutsk, 7. 1990, leg. Smirnov: 18 ♀ ♀ ad., 9 ♀ ♀ juv. Chita, sand-pit, 9. 9. 1991, leg. Smirnov: more than 70 ♀ ♀ ad., 70 ♀ ♀ juv., 100 ♂ ♂, 40 ♀ ♀ e.

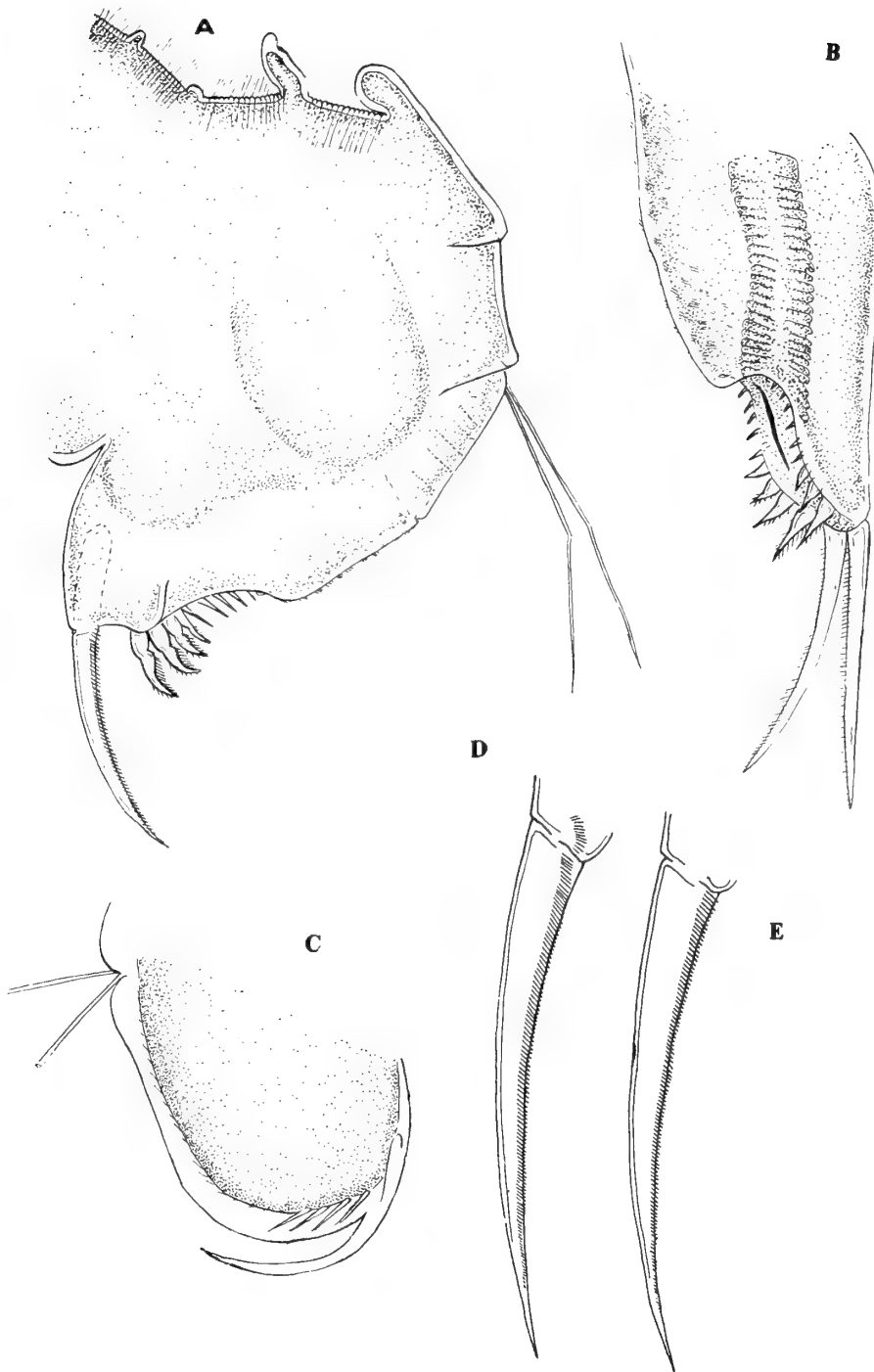


Fig. 12 *S. vetulus*, female postabdomen. A, lateral view, B, dorsal view, C, postabdomen of neonate, D, outer side of postabdominal claw, E, inner side of postabdominal claw.

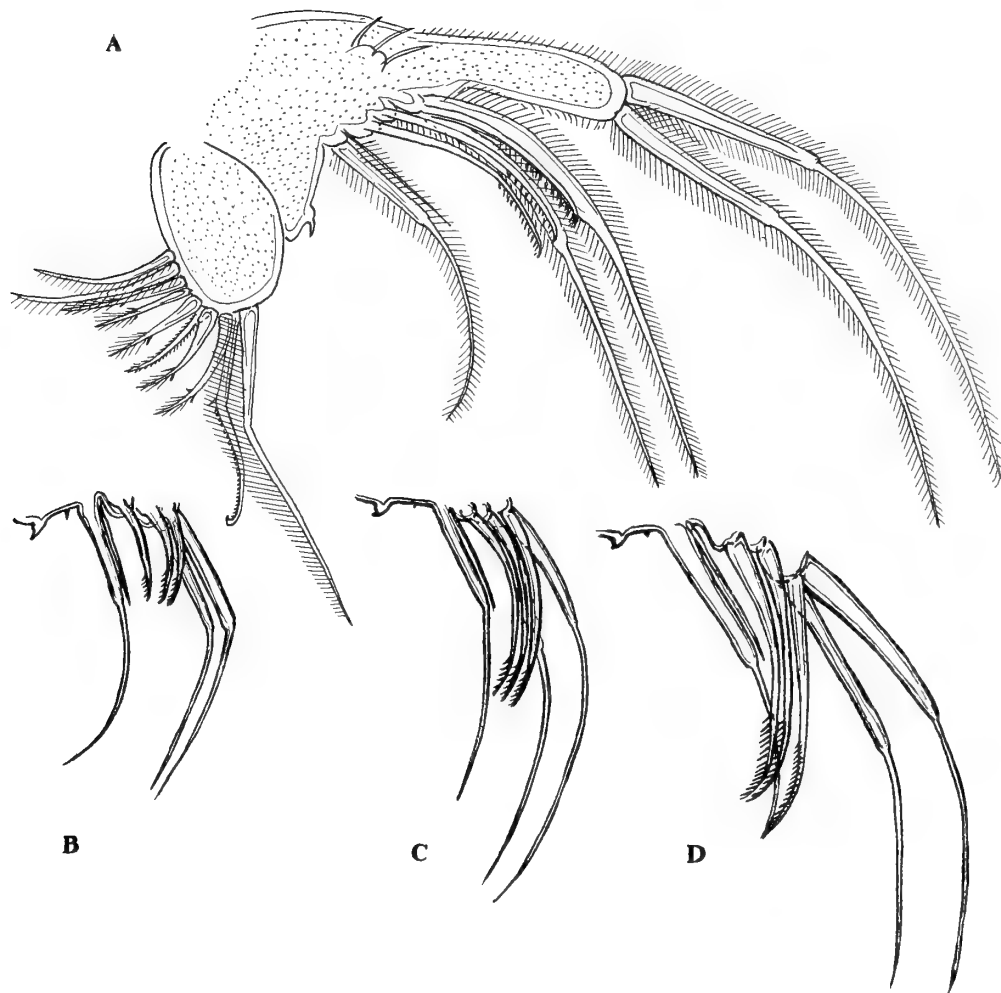


Fig. 13 *S. vetulus*, male 2nd trunk limb. A, general view, B, endite of neonate, C, endite of juvenile, D, endite of adult.

Kolyma river basin, Zhirkovo lake, 28. 6. 1967, leg. Streletskaia: 4 ♀ ♀ ad., 2 ♀ ♀ e. Magadan region, Verkhnee lake, 18. 8. 1981, leg. Streletskaia: 13 ♀ ♀ ad., 8 ♀ ♀ juv.

DIAGNOSIS. Measurements. ♀ ♀ ad.: 1.3–2.4 mm., ♀ ♀ e.: 1.2–1.9 mm, ♂ ♂: 1.0–1.3 mm.

Female. Dorso-posterior valve prominence long, with very wide base and small diameter (Fig. 24). Its diameter (Fig. 2) less than its length. Dorsal valve margin very high, not protruding backward. Depressions above and below dorso-posterior prominence wide and deep. Ventral head margin straight or slightly concave, sometimes with small prominence. Depression on ventral head margin near rostrum deep. Ocellus elongate.

DISTRIBUTION. (Fig. 21) Eastern Siberia *S. vetuloides* has been described from the Jana river basin. Sars (1903) reports it also from Kazakhstan. However, the illustration in this article shows that the specimens found in Kazakhstan belong to *S. mixtus*. *S. vetuloides* is reported from China (Chiang & Du, 1979), Mongolia (Flössner, 1986) and South Africa (Sars, 1916). But the identification of species within the subgenus *Simocephalus* s. str. is rather difficult. And probably the name *S. vetuloides* was misused for other species.

REMARKS. Behning (1941) and Manujlova (1964) suppose *S. vetuloides* to be a synonym of *S. elizabethae*. Other authors (Fryer,

1957; Negrea, 1983; Michael & Sharma, 1988) regard it as a synonym of *S. vetulus*. Investigation of the type material and other specimens shows that it is a separate species. It is sympatric with *S. mixtus* and there are no intermediate forms between these species. *S. vetuloides* differs from *S. vetulus* in the shape of the dorso-posterior valve prominence and from *S. elizabethae* in the head shape.

Contrary to the opinion of Manujlova (1964), the length of the distal seta of the antennal basipod does not differ in this species from the others (Fig. 24B). The basipod bears a seta on the outer and a spine on the inner side of the distal part.

S. punctatus sp. nov.

Fig. 25

TYPE MATERIAL. Holotype: Shallow eutrophic vernal pool in river bottom below a dam on the Friant River, Tulare Co. California, 37°N 119°45'W, leg. Berner: MPA: ♀ ad. (BMNH) 1997. 1698. Paratypes collected with holotype: MPA: more than 50 ♀ ♀ ad., 20 ♀ ♀ juv., 20 ♀ ♀ e., 20 ♂ ♂ (BMNH 1997. 1699–1708 and AC).

DIAGNOSIS. Measurements. ♀ ♀ ad.: 1.5–2.23 mm., ♀ ♀ e.: 1.2–1.9 mm, ♂ ♂: 1.1–1.3 mm.

Female. Dorso-posterior valve prominence absent, dorso-posterior angle not separated above and below by depressions (Fig. 25).



Fig. 14 *S. vetulus*, male postabdomen. A, lateral view, B, distal part, C, supra-anal angle with vas deferens.

Diameter of circle inscribed in it large. Dorsal valve margin low, not protruding backward. Ventral head margin straight or slightly concave, sometimes with small prominence. Depression on ventral head margin near rostrum deep. Ocellus point-like.

ETYMOLOGY. The name '*punctatus*' refers to the point-like ocellus that is typical of this species.

REMARKS. The shapes of the head and valves are similar in *S. punctatus* and *S. vetulus*. The former species differs distinctly from the latter, and from all other species of this subgenus, in the shape of the ocellus, which is point-like in all available specimens of *S. punctatus*.

S. gibbosus Sars, 1896

Fig. 26

Simocephalus gibbosus Sars, 1896: 15; *S. vetulus gibbosus*: Dumont, 1983: 102.

TYPE MATERIAL. Lectotype (designated here): Australia, Sydney, Centennial park: CBS: ♀ ad. (ZMO, F 9766, Mp. 170). Paralectotypes collected with lectotype: 5 ♀ ♀ ad. (ZMO, F 9766, Mp. 170), MPA: 15 ♀ ♀ ad. (ZMO, F 19261).

MATERIAL EXAMINED (Fig. 21). Lectotype, paralectotypes and other specimens: more than 250 specimens (♀ ♀ ad. and ♀ ♀ juv.)

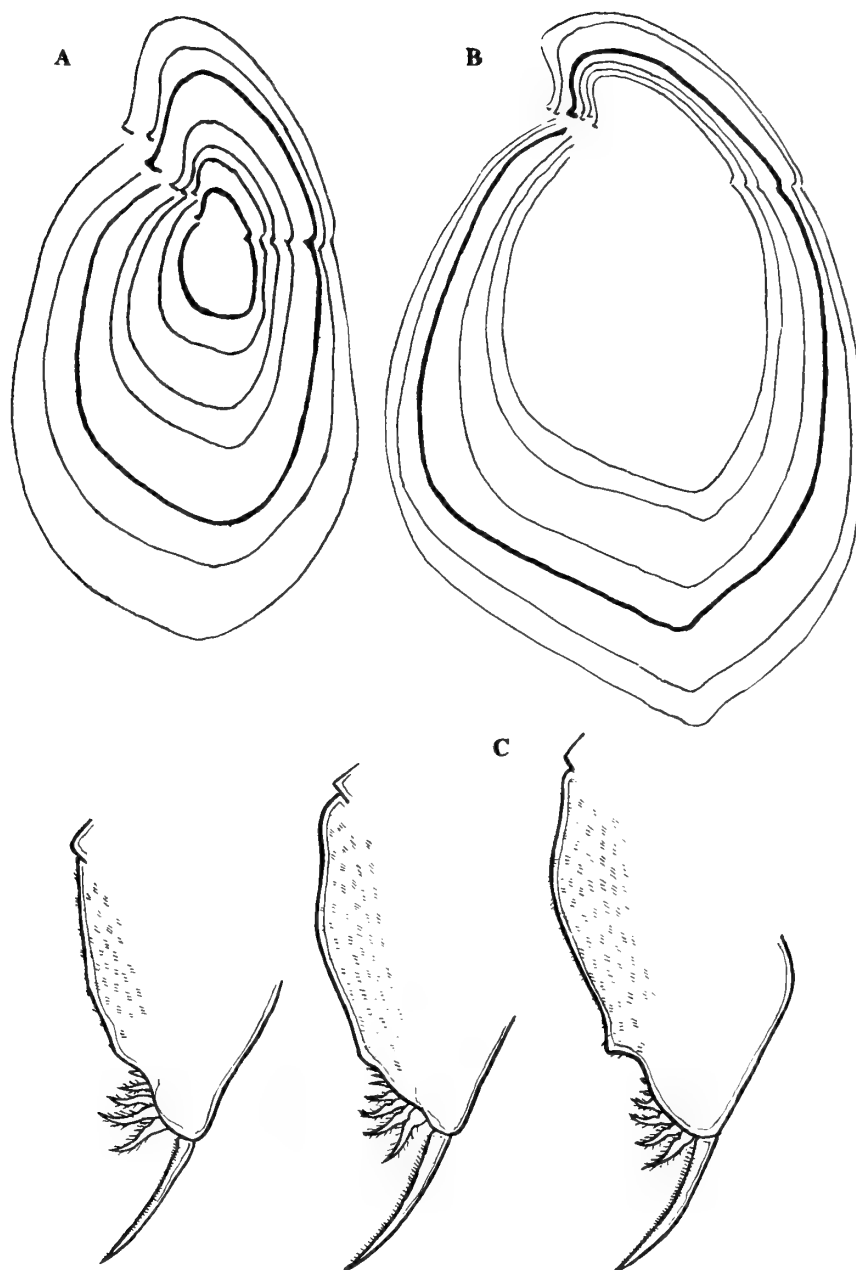


Fig. 15 Age variation in shape. A, *S. vetulus* female, B, *S. exspinosus* female, C, *S. vetulus* male postabdomen.

from 11 localities in Australia: New South Wales, Victoria, Queensland, Northern Territory. The material is in AM and AC.

DIAGNOSIS. Measurements. ♀ ♀ ad.: 1.0–2.4mm., ♀ ♀ e.: 1.2–1.9. Female. Dorso-posterior valve prominence long, with very wide base and small diameter (Fig. 26). Its diameter less than its length (Fig. 2). Dorsal valve margin very high, protruding backward strongly. Depressions above and below dorso-posterior prominence wide and deep. Ventral head margin always with prominence, without depression under eye. Depression on ventral head margin near rostrum very shallow, sometimes absent. Ocellus elongate. Male. unknown.

DISTRIBUTION. (Fig. 21) Australia.

REMARKS. The original description of this species (Sars, 1896) is comprehensive and provided with good illustrations. Dumont (1983) supposes *S. gibbosus* and *S. elizabethae* to be subspecies of *S. vetulus*. Examination of *S. gibbosus* type material and specimens of *S. elizabethae* shows that these species differ from *S. vetulus* in the shape of the valves and head. In addition, they are sympatric and consequently cannot be subspecies of one species.

S. elizabethae (King, 1853)

Fig. 27

Daphnia Elizabethae King, 1853a: 247; *Simocephalus vetulus*: Schödler, 1877: 18 partim, Negrea, 1983: 138 partim; *S. vetulus elizabethae*: Dumont, 1983: 98; *S. dulvertonensis* Smith, 1909: 81.

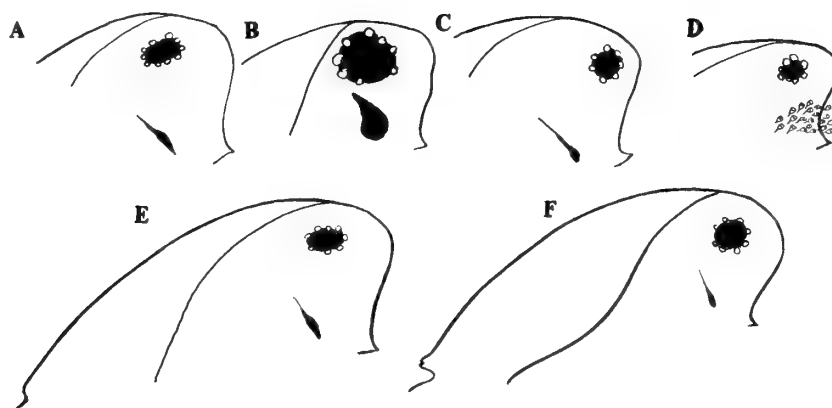


Fig. 16 *S. vetulus*, variation. A–C, variation of ocellus size, A, female collected 12. 5. 1990, B, female collected 5. 9. 1990, C, female from the same sample after 17 days in room temperature, D, head covered with epibionts, E, head without prominence in dorso-posterior part, F, head with prominence in dorso-posterior part.

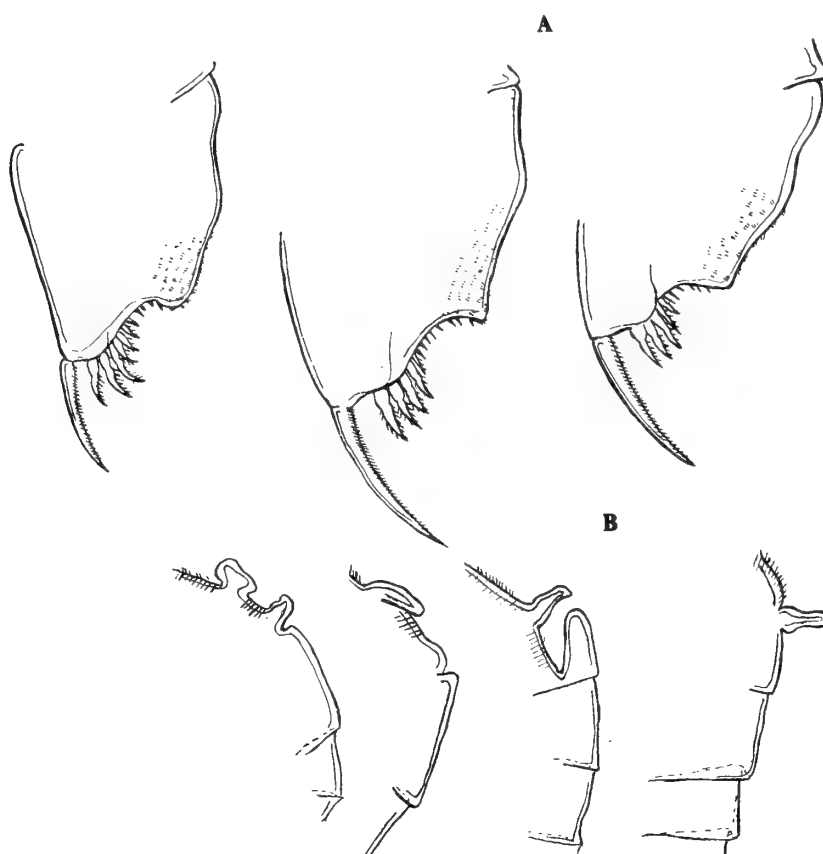


Fig. 17 *S. vetulus*, variation of abdomen and postabdomen, female. A, postabdomen, B, abdominal processes.

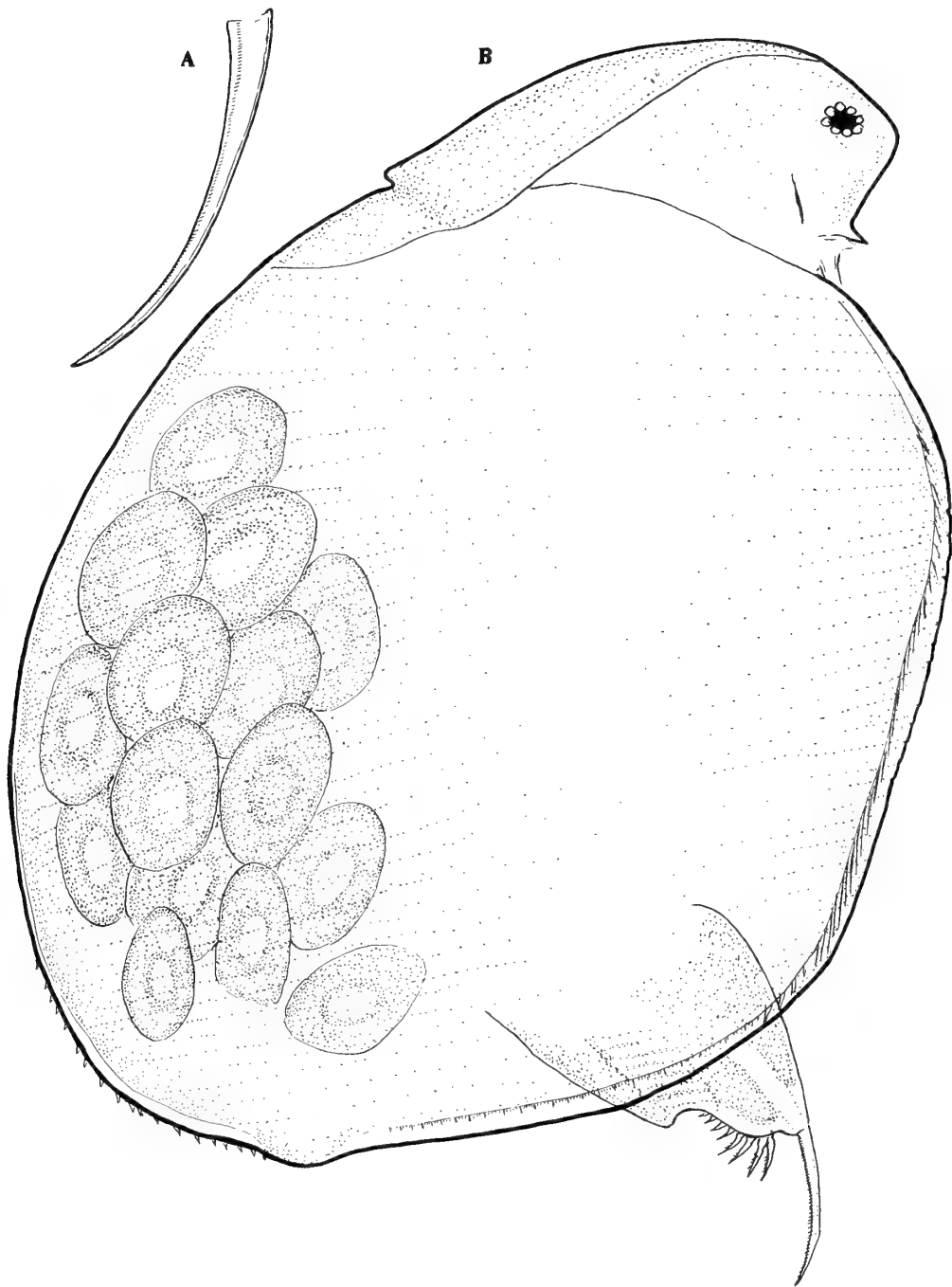


Fig. 18 *S. vetulus*, neotype, parthenogenetic female. A, postabdominal claw, B, lateral view.

TYPE MATERIAL. Types were probably not preserved by King. At least, they are not to be found in AM, SAM and MV. The specimens were from Sydney, New Town, Parramatta, the Cowpastures, and from River Karuah, near Stroud, Port Stephens. Type locality not indicated in the original description (King, 1853a).

MATERIAL EXAMINED. More than 550 specimens (♀ ♀ ad., ♀ ♀ juv., ♀ ♀ e., ♂ ♂) from 15 localities in Tasmania, New Guinea and Australia (New South Wales, South Australia, Western Australia, Victoria, Northern Territory, Queensland) (Fig. 21) (AM, SAM, MV).

DIAGNOSIS. Measurements. ♀ ♀ ad.: 1.2–3.4 mm., ♀ ♀ e.: 1.2–1.9, ♂ ♂: 1.1–1.3 mm.

Female. Dorso-posterior valve prominence long, with very wide base and small diameter (Fig. 27): diameter less than its length (Fig. 2). Dorsal valve margin very high, not protruding backward. Depressions above and below dorso-posterior prominence wide and deep. Ventral head margin with depression just under eye. Depression on ventral head margin near rostrum shallow, sometimes absent. Ocellus elongate.

DISTRIBUTION. (Fig. 21) Australia, Tasmania, New Guinea. The species is reported from Ceylon (Daday, 1898), Sumatra, Java,

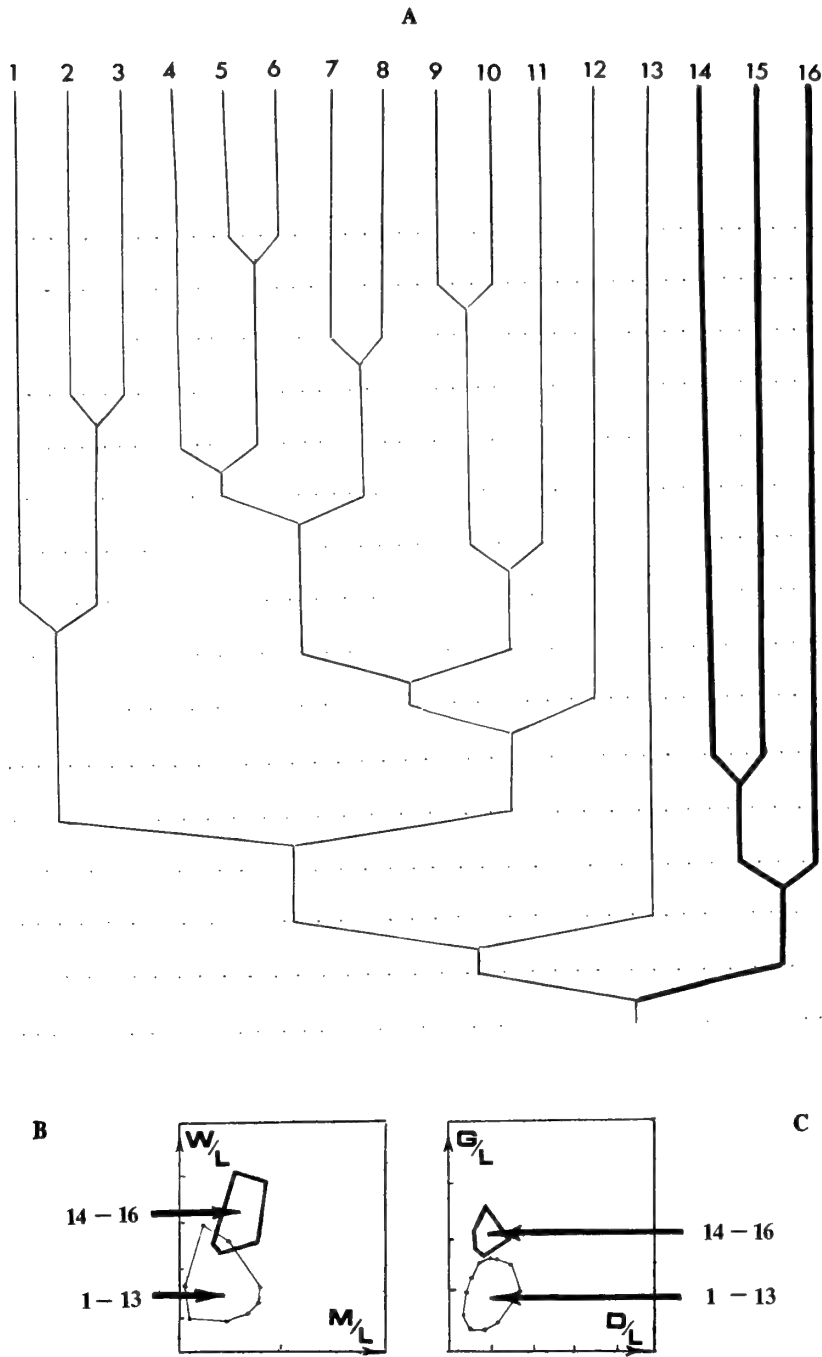


Fig. 19 Statistical analysis of 16 series of *Simocephalus* s. str. from Europe. 1–13 – *S. vetulus*, 14–16 – *S. mixtus*. A, result of cluster analysis, B, C, diagrams of characters.

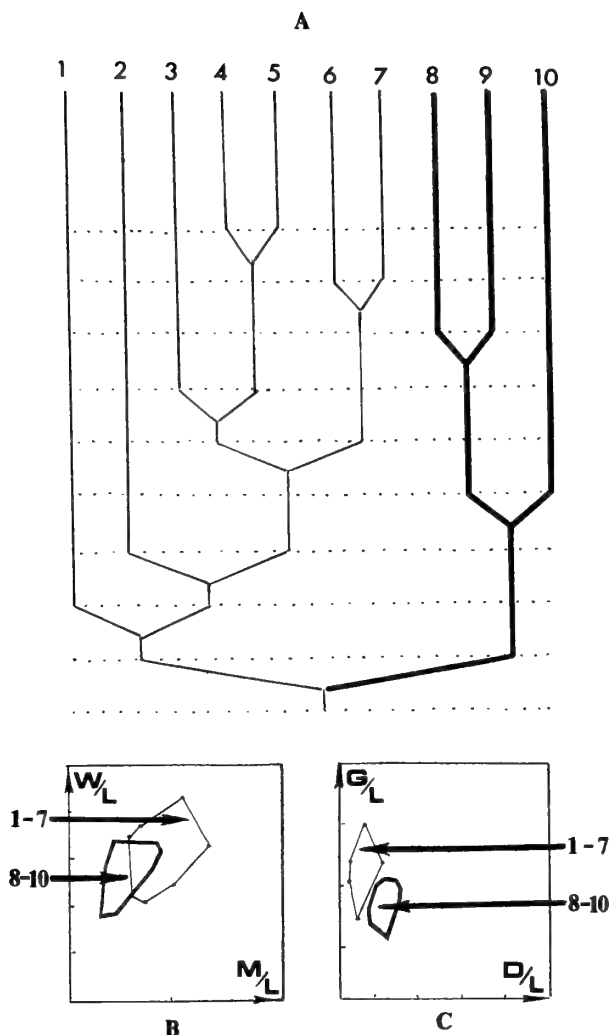


Fig. 20 Statistical analysis of ten series of *Simocephalus* s. str. from East Siberia and Far East. 1–7 – *S. vetuloides*, 8–10 – *S. mixtus*. A, result of cluster analysis, B, C, diagrams of characters.

China (Stingelin, 1904), India (Biswas, 1971), Niger (Dumont & Van De Velde, 1977a), Nepal (Dumont & Van De Velde, 1977b), Central Asia (Manujlova, 1964). But judging from illustrations, these authors had specimens not of *S. elizabethae* but of *S. mixtus*.

REMARKS. The original description (King, 1853a) contains the characters of two species. The first adequate description of this species was made by Sars (1888). Schödler (1877) and Negrea (1983) suppose *S. elizabethae* to be a synonym of *S. vetulus*. Dumont (1983) regards it as a subspecies of *S. vetulus*. I believe *S. elizabethae* to be a separate species, because it differs from *S. vetulus* in the shape of the ventral head margin and dorso-posterior valve prominence. These differences are not less than the differences between other species within this subgenus.

Judging from the original description (Smith, 1909), the Tasmanian species *S. dulvertonensis* belongs to *Simocephalus* s.str. Information about the type material is lacking. Available specimens from Tasmania differ slightly from Australian material in the shape of the dorso-posterior valve prominence, but this difference is insufficient to assign them to a separate species or subspecies. I agree with Brehm (1953) and Dumont (1983), that *S. dulvertonensis* is a synonym of *S. elizabethae*.

Subgenus *S. (Echinocaudus)* subgen. nov.

TYPE SPECIES. *Simocephalus exspinosus* (De Geer, 1778).

DIAGNOSIS. Both sexes (Figs 28; 29). Frons rounded or pointed, without denticles. Head shield without depression. Head pores present. Insertion of antennules at base of rostrum. Antennule long or short in correspondence with long or short rostrum, with neither ridges nor denticles on inner side. Aesthetes longer than base of antennule. Postabdominal claw with basal pecten of spines at outer side. Inner side and distal part of outer side with fine setules. Anal bay of postabdomen narrow, rounded, with anal teeth.

Female. Dorso-posterior valve angle with rounded prominence or without it. Valves without dorsal keel. Posterior corner of ephippium without protuberance. Ocellus short. Setae of 2nd and 3rd endite prominence of 2nd trunk limb as long as 0.7 and 1.1 of basal segment of plumose seta of 1st prominence respectively (Fig. 30B). Postabdomen with 9–22 anal teeth on each side (Fig. 28C). Supra-anal angle rounded.

Male. Supra-anal angle rounded (Fig. 29). Vas deferens opening near its base. Postabdomen with 5–6 anal teeth on each side. Dorso-posterior valve angle with rounded or pointed prominence.

ETYMOLOGY. The name '*Echinocaudus*' is derived from the words '*echinus*' – 'hedgehog' and '*cauda*' – 'tail' and refers to the pecten of spines at the base of postabdominal claw that is typical of this subgenus.

S. obtusatus (Thomson, 1878)

Fig. 31

Daphnia obtusata Thomson, 1878: 261; *Simocephalus obtusatus*: Sars, 1894.

TYPE MATERIAL. No information. Type locality: New Zealand, Dunedin.

MATERIAL EXAMINED. New Zealand, Lake Takapuna, leg. Henry: ♀ ad. (AM, 7182).

DIAGNOSIS. Measurements. ♀ ♀ ad.: 2.0–2.5 mm. ♂ ♂: 1.0–1.2 mm. Both sexes. Frons rounded (Fig. 31D). Ventral head margin very convex. Rostrum short. Setules on inner side of posterior valve margin slender. Dorso-posterior valve angle without prominence (Fig. 31A,F). One supra-anal angle (Fig. 31E). Basal pecten of postabdominal claw with 10–12 large well-spaced spines (Fig. 31C). Size of spines maximal in middle.

DISTRIBUTION. (Fig. 32) New Zealand.

REMARKS. The original description was provided with an illustration and shows that *S. obtusatus* differs markedly from all other

species in head shape (Thomson, 1878). The most detailed description of the female and the first description of the male was given by Sars (1894).

S. daphnoides Herrick, 1883

Fig. 33

Simocephalus daphnoides Herrick, 1883: 503; *S. Iheringi* Richard, 1897: 279 syn. nov.; *S. fonsecai* Bergamin, 1939: 82 syn. nov.; *S. fonsecai* var. *sinucristatus* Bergamin, 1939: 84 syn. nov.

TYPE MATERIAL. Probably the types were not indicated by Herrick as in the case of other species described by this author (D. Frey, personal communication through N.N. Smirnov). Type locality: U.S.A., Alabama, Decatur.

MATERIAL EXAMINED. Argentina, Rio Parana, Catay pond, 1973, leg. Frutos: 3 ♀ ♀ ad., 3 ♀ ♀ juv. (AC). Peru, vicinity of Pucallpa, pond near Ucayali river, 2. 1987, leg. Pegasov: 4 ♀ ♀ ad. (AC).

DIAGNOSIS. Measurements. ♀ ♀ ad.: about 1 mm.

Female. Frons rounded (Fig. 33). Ventral head margin concave, straight or with small prominence. Rostrum short. Setules on inner side of posterior valve margin slender. Dorso-posterior valve angle with large, pointed prominence. One supra-anal angle. Basal pecten of postabdominal claw of 20–30 small, close-set spines of equal length.

Male unknown.

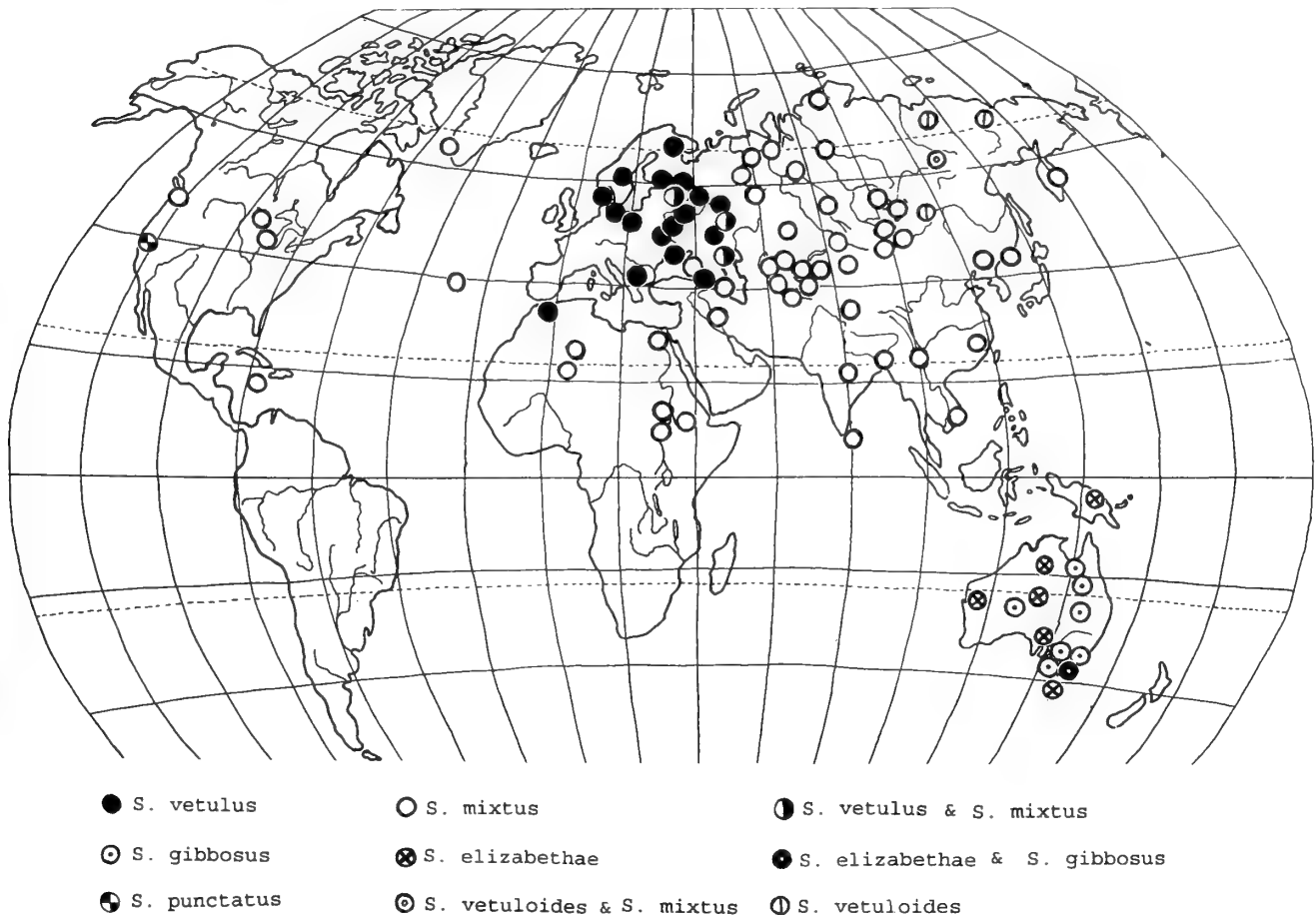


Fig. 21 Locations, where studied material of *Simocephalus* s. str. was collected.

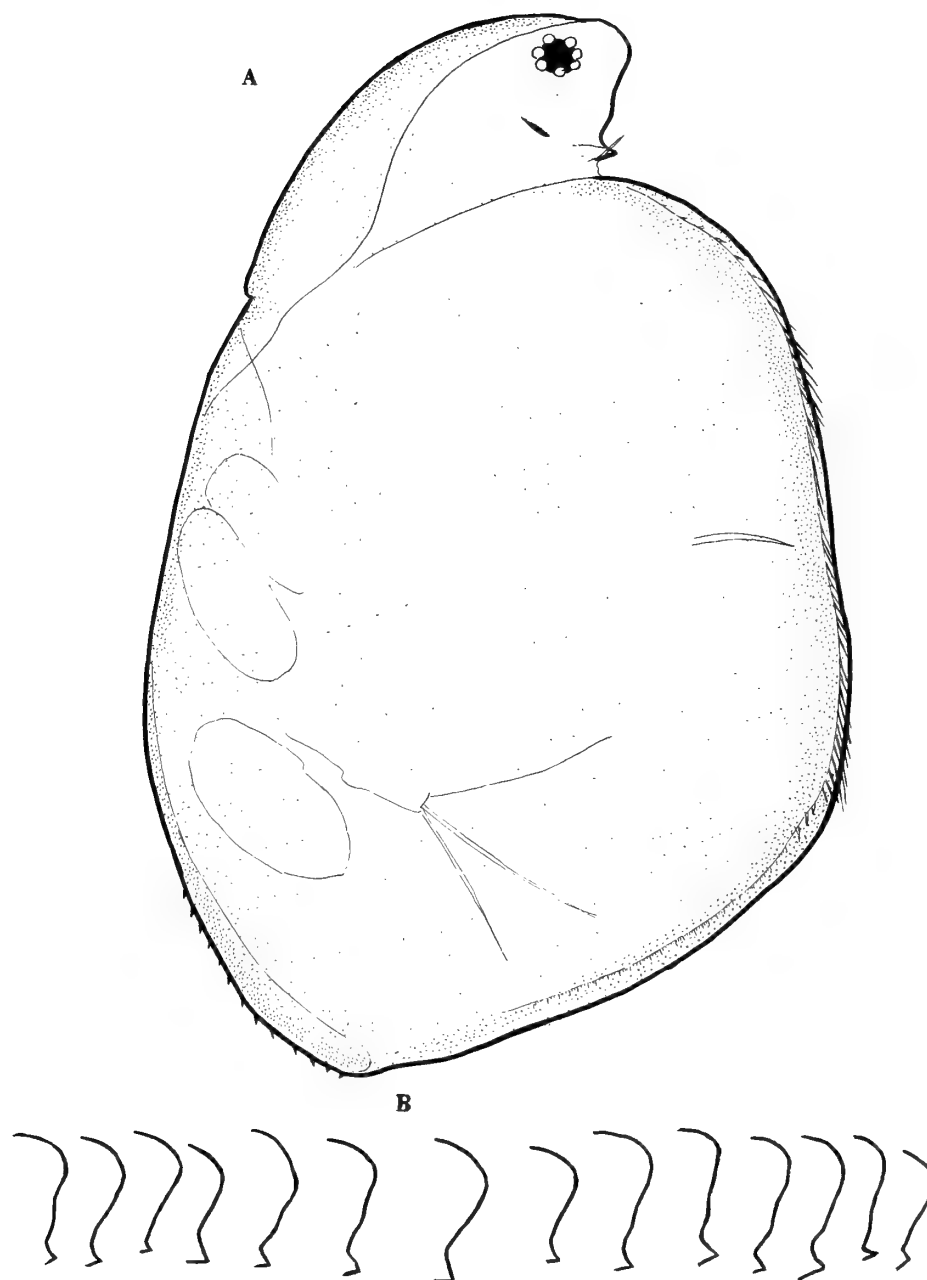


Fig. 22 *S. vetulus* var. *angustifrons* (= *S. vetulus*), type series. A, parthenogenetic female, lectotype, B, variability of ventral head margin.

DISTRIBUTION. (Fig. 32). U.S.A., Alabama (Herrick, 1883), Argentina (Sars, 1901 and our data), Brasil (Richard, 1897), Paraguay, Columbia (Olivier, 1960), Peru (our data).

REMARKS. The original description of this curious species is short but provided with a good illustration (Herrick, 1883). Obviously, *S. daphnoides* is the senior synonym of *S. iheringi*. The latter name is used (Olivier, 1960) while the former name has been forgotten. *S. iheringi* was described from Brasil (Richard, 1897). There is no information about the types. The male was originally described by Sars (1901).

S. fonsecai and *S. fonsecai* var. *sinucristatus* were described from Brasil. There is no information about the types. Harding (1955) supposes *S. fonsecai* to be a synonym of *S. iheringi*. The original description (Bergamin, 1939) supplied with the lateral view of both

varieties and the view of the postabdomen of *S. fonsecai* shows that both names are junior synonyms of *S. daphnoides*.

S. (EXSPINOSUS) species group

DIAGNOSIS. Both sexes (Figs 28–30). Frons rounded. Ventral head margin concave, straight or with small prominence. Rostrum short. Setules on inner side of posterior valve margin slender. Dorso-posterior valve angle without prominence or with small rounded prominence. One supra-anal angle. Basal pecten of postabdominal claw of 8–25 close-set spines of equal length.

S. exspinosus (De Geer, 1778)

Figs 28–30

Monoculus exspinosus De Geer, 1778: 457; *Daphnia exspinosus*: Koch, 1841: 35; *Daphnia sima*: Lievin, 1848; Baird, 1850: 95; *Simocephalus exspinosus* Schödler, 1858: 20; Lilljeborg, 1900: 177; *Daphnia australiensis* Dana, 1852: 1271; Sars, 1888: 15; *S. exspinosus australiensis*: Dumont, 1983: 104; *S. sibiricus* Sars, 1898: 329 syn. nov.; *S. productus* Sars, 1903: 173; *S. himalayensis* Chiang & Chen, 1974: 129 syn. nov.; *S. vamani* Rane, 1985b: 225.

TYPE MATERIAL. The types appear to be lost. There are no specimens of this species in the collection of De Geer deposited in the Museum of Natural History in Stockholm (L. Sandberg, curator of Crustacea, personal communication). The type locality is not indicated in the original description (De Geer, 1778).

MATERIAL EXAMINED. Type material of junior synonyms: *S. sibiricus* Sars, 1898: Lectotype (designated here): Russia, Siberia, Verkhoyansk, 1885: MPA: ♀ ad. (ZICC, 4691). Paralectotypes collected with lectotype: 9 ♀ ♀ ad. (ZICC, 4691). *S. productus* Sars, 1903: Lectotype (designated here): Kazakhstan, Akmolinsk region: MPA: ♀ ad. (ZICC, 7098). Paralectotypes collected with lectotype: 35 ♀ ♀ ad. (ZICC, N7098). Other specimens: more than 1000 specimens (♀ ♀ ad., ♀ ♀ juv., ♀ ♀ e., ♂ ♂) from 56 localities in Russia, Ukraine, Georgia, Kazakhstan, Uzbekistan, Tadjikistan, Mongolia,

China, India, Pakistan, Bangladesh, Egypt, Algeria, Rwanda, South Africa and Australia. Material is deposited in AC, ZICW, ZICC, MCA, SAM, AM. Some specimens are selected from the samples from ZIPD.

DIAGNOSIS. Measurements. ♀ ♀ ad.: 1.8–3.5 mm., ♀ ♀ e.: 1.2–1.9 mm. ♂ ♂: 1.0–1.3.

Female. (Fig. 28). 12–22 anal teeth. Prominence of dorso-posterior valve angle small or absent. Basal pecten of postabdominal claw of 8–12 spines of moderate size.

DISTRIBUTION. This species is assumed to be cosmopolitan by many authors, but its range needs to be redefined. It occurs with certainty in Europe, Asia, Africa, Australia (Fig. 32). The available specimens from different continents belong to one morphological species. Unfortunately, I have no specimens from America.

REMARKS. The original description of *S. exspinosus* is very short: 'Monoculus exspinosus branchiis dichotomis cauda simplici inflexa testa postice rotundata non spinosa' (De Geer, 1778). This is appropriate for any species of *Simocephalus*. Koch and Schödler are often erroneously thought to be the authors of the species, because Koch (1841) described and drew it and Schödler (1858) was the first to

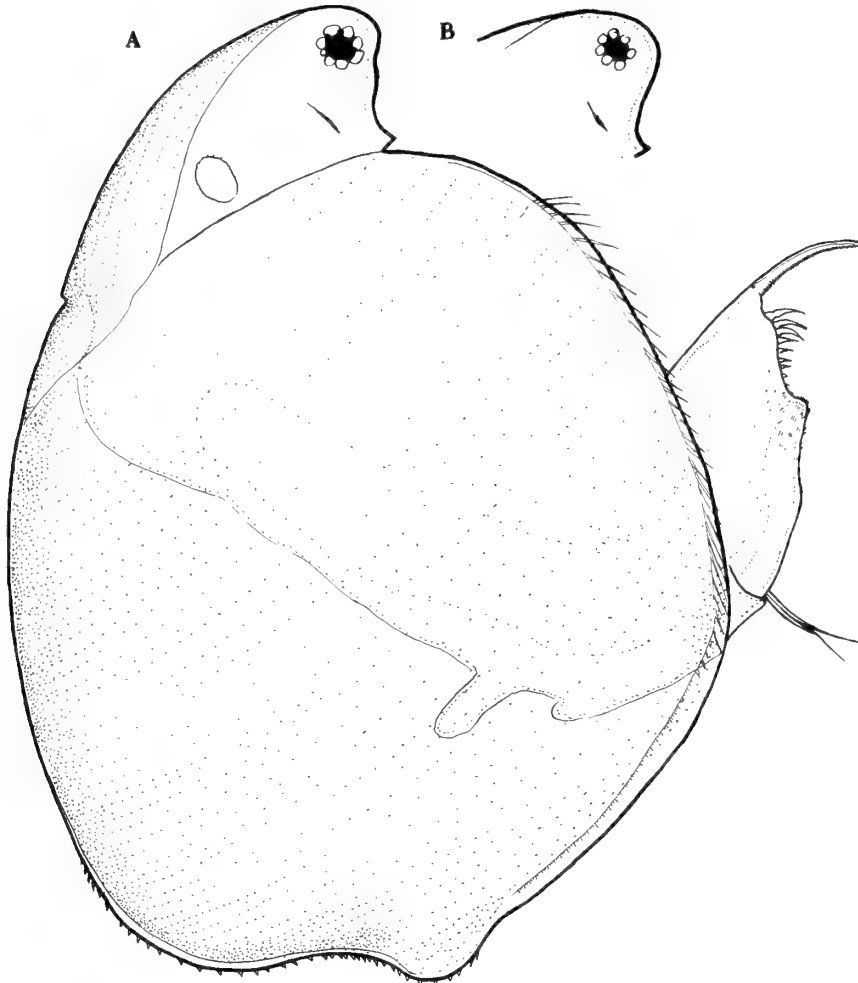


Fig. 23 *S. mixtus*, type series A, parthenogenetic female, lectotype, B, ventral part of the head of paralectotype.

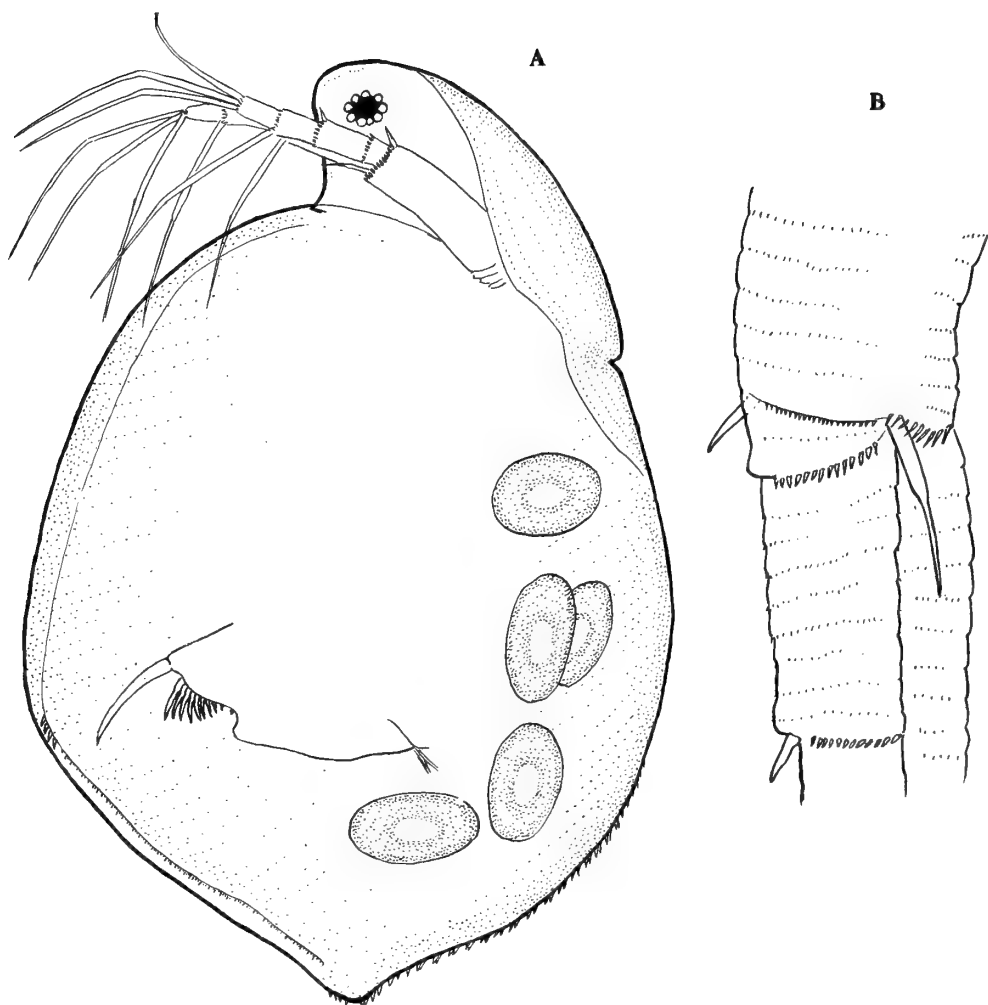


Fig. 24 *S. vetuloides*, lectotype, parthenogenetic female. A, general view, B, distal part of antenna basipod with a seta on outer side and a spine on inner side.

assign it to the genus *Simocephalus*. But their descriptions are insufficient. Some authors supposed *S. exspinosus* to be the junior synonym of *S. vetulus* (*Daphnia sima*) (Lievin, 1848; Baird, 1850). Lilljeborg (1900) was the first to describe this species appropriately.

S. australiensis was originally described insufficiently (Dana, 1852). Dana's collection with the type was lost on a ship which sank (D. Frey, personal communication through N.N. Smirnov). Sars is often supposed to be the author of this species (Negrea, 1983) because he is the first to describe it appropriately (Sars, 1888). He believed *S. australiensis* to be a separate species closely related with *S. exspinosus* and differing from it by 'the peculiar oblique form of the carapace and well-marked, though obtuse, projection of its posterior extremity; likewise too by the broad tail, and more especially by the highly characteristic armature of the caudal claws'. Dumont (1983) regards *S. australiensis* as a subspecies of *S. exspinosus*. Other authors regard it as a synonym (Flössner, 1972; Negrea, 1983; Margaritora, 1985; Michael & Sharma, 1988). I agree with the latter opinion, because the diagnostic characters used by Sars and Dana are rather variable and because all available specimens of the *S. (exspinosus)* species group from Australia do not differ from European *S. exspinosus*.

According to Sars (1898, 1903), *S. sibiricus* and *S. productus* differ from each other and from *S. exspinosus* in the head shape, the

size of the dorso-posterior valve prominence and the armature of the postabdominal claw. Manujlova (1964) mentions *S. sibiricus* as a separate, highly variable species. Judging from illustrations, she confuses two species under this name. *S. productus* is believed to be a synonym of *S. exspinosus* (Manujlova, 1964; Michael & Sharma, 1988). Investigation of the type has shown that *S. productus* and *S. sibiricus* do not differ from *S. exspinosus*. The frons shape varies from rounded to almost right-angled. The head height also varies within populations. Therefore these features cannot be diagnostic characters.

S. himalayensis is described from the Himalayas (Chiang & Du, 1979). The type is in China and I have not seen it. Reference to the original description and illustrations suggests that *S. himalayensis* is a synonym of *S. exspinosus*.

According to Rane (1985b), *S. vamani*, described from Jabalpur (India) differs from *S. exspinosus* in its moderate size, a comparatively small rostrum, and the presence of 6–7 denticles on the postabdomen near the insertion of the claw. This author also states that *S. austarliensis* differs from *S. vamani* in the upturned rostrum. According to my data, the group of 6–7 denticles near the claw occurs in all *Simocephalus* species and the size and orientation of the rostrum is subject to individual variability. The type is deposited in the National collection of the Zoological Survey of India (Calcutta).

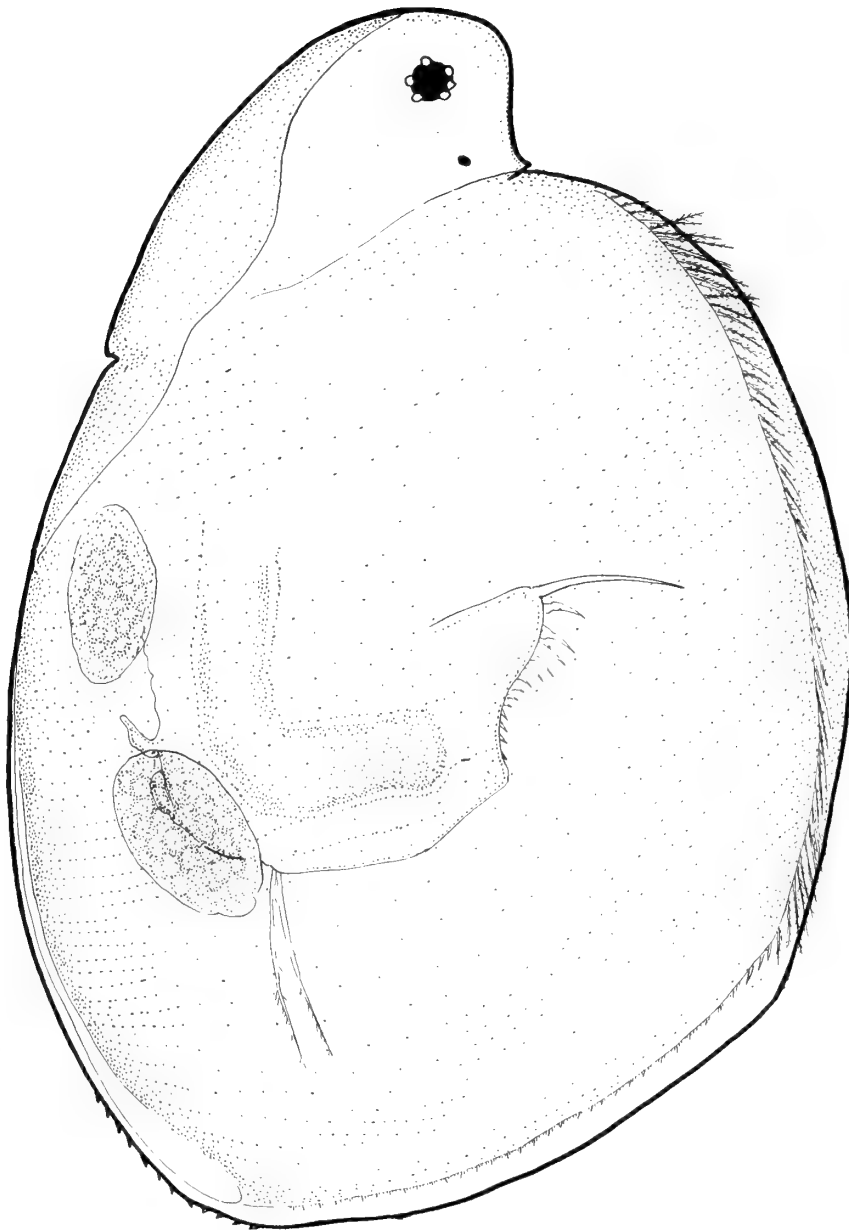


Fig. 25 *S. punctatus* sp. nov., holotype, parthenogenetic female.

Sharma & Sharma (1990) sink *S. vamani* into the synonymy of *S. exspinosus* on the base of the investigation of the type. I agree with them because all available specimens of the *S. (exspinosus)* group from India belong to *S. exspinosus*.

***S. congener* (Koch, 1841)**

Fig. 34

Daphnia congener Koch, 1841: 35; *Simocephalus congener*: Schödler, 1858: 20; Šrámek-Hušek *et al.*, 1962: 265; *S. exspinosus* var. *congener*: Lilljeborg, 1900: 177; *S. exspinosus*: Sars, 1888: 16; Flössner, 1972: 184.

TYPE MATERIAL. The types appear to be lost. Type locality not indicated in the original description. Probably it is in Germany.

MATERIAL EXAMINED. Russia, Moscow region, Ruza district, Terekhovskiy pond near Glubokoe lake, 29. 7. 1983, 29. 7. 1983, leg. Korovchinsky., 19. 8. 1989, leg. Orlova-Bienkowskaja: more than 20 ♀ ♀ ad., 20 ♀ ♀ juv., 10 ♀ ♀ e. Vicinity of the Lake Baikal, Maloe More, pool at the swamp, 19. 8. 1982, leg. Glagolev: 10 ♀ ♀ ad., 14 ♀ ♀ juv. Vicinity of the Lake Baikal, Proval, water-meadow at Oblom, 20. 8. 1982, leg. Glagolev: 2 ♀ ♀ ad. All series are in AC.

DIAGNOSIS. Measurements. ♀ ♀ ad.: 1.5–2.2mm, ♀ ♀ e.: 1.2–1.8mm. Female. (Fig. 34). 9–18 anal teeth. Prominence of dorso-posterior valve angle absent. Basal pecten of postabdominal claw of 20–25 small spines.

DISTRIBUTION. (Fig. 32) This species was previously confused with *S. exspinosus*, so its range needs to be redefined. It occurs with certainty in Central and Eastern Europe and Siberia.

REMARKS. The original description of *S. congener* is insufficient (Koch, 1841). Lilljeborg (1900) was the first to describe it appropriately, though this author believes this species to be a variety of *S. exspinosus*. Most authors suppose *S. congener* to be a synonym of *S. exspinosus* (Sars, 1888; Flössner, 1972; Margaritora, 1985; Sharma & Michael, 1988) or a variety (subspecies) (Behning, 1941). But Šrámek-Hušek *et al.* (1962) regard it as a separate species. I believe the latter opinion to be correct because there is a morphological hiatus between *S. exspinosus* and *S. congener* in the number and size of spines on the postabdominal claw. In addition, these species are sympatric in Europe.

S. (ACUTIROSTRATUS) species group

Female (Fig. 35). Frons pointed. Ventral head margin concave. Rostrum long. Setules on inner side of posterior valve margin thick. Dorso-posterior valve angle without prominence or with rounded prominence. Two supra-anal angles. Basal pecten of postabdominal claw of 10–15 large, close-set spines, which increase in size distally. Male. Unknown.

S. acutirostratus (King, 1853)

Fig. 35

Daphnia Elizabethae var. *acuti-rostrata* King, 1853b: 254; *Simocephalus acutirostratus*: Sars, 1896: 12; *S. paradoxus* Schödler, 1877; *S. vidyae* Rane, 1983: 154; *S. vidyae gajareae* Rane, 1986: 168.

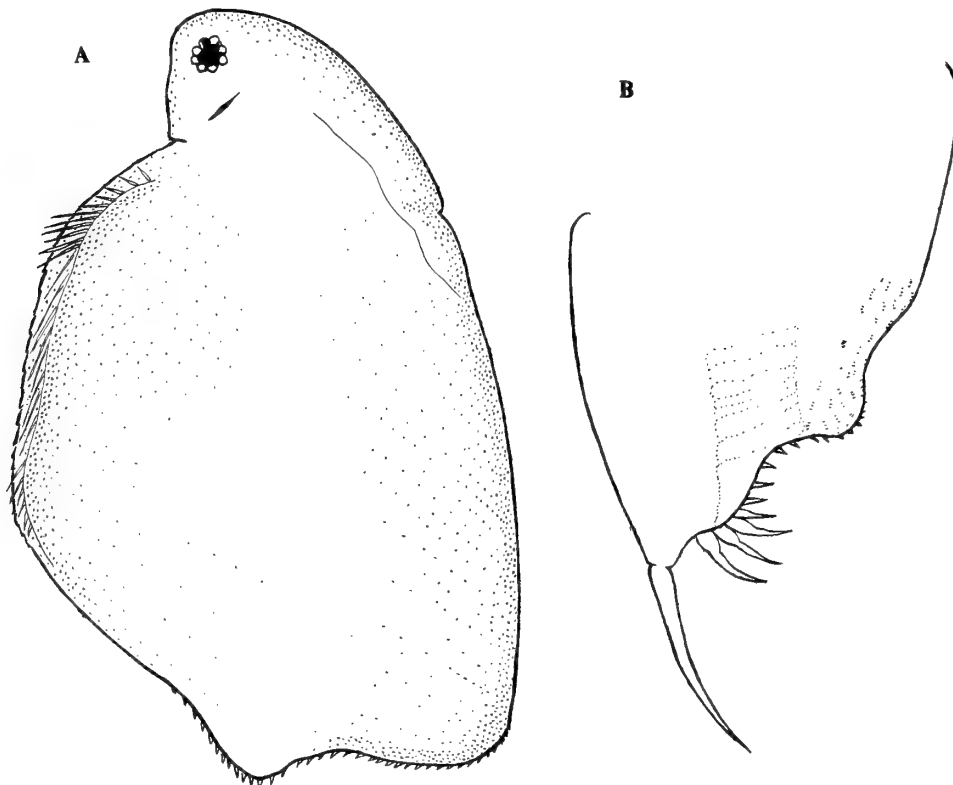


Fig. 26 *S. gibbosus*, lectotype, parthenogenetic female. A, lateral view, B, postabdomen.

TYPE MATERIAL. Type probably not indicated by King. Type locality: Australia, New South Wales, ponds in Denham Court.

MATERIAL EXAMINED. (Fig. 32) Australia, New South Wales, swamp 26km east of Cobar, 31°30'S 146°7'E, 12. 12. 1973, leg. Timms: more than 20 ♀ ♀ ad., 20 ♀ ♀ juv. New South Wales, Casino, 28°52'S 153°3'E, leg. Henry: ♀ ad. New Caledonia, dam near La Foa, 21°50'S 166°53'E, 8. 8. 1981, leg. De Deckker: ♀ juv. Queensland, pool at the road side, 30. 6. 1974: 2 ♀ ♀ ad., 5 ♀ ♀ juv. Queensland, Lake Lalilee, 22°19'S 145°51'E, 22. 4. 1984, leg. Timms: ♀ ad. Material in AM and AC.

DIAGNOSIS. Measurements. ♀ ♀ ad.: 1.0–3.0mm.

Female. General body shape ovoid (Fig. 35). Frons with large sharp prominence. Dorso-posterior valve prominence distinct, separated above and below with shallow, wide depressions. Diameter of circle inscribed in it large. Dorsal margin with denticles. Proximal and distal supra-anal angles large, embayments of postabdomen deep, proximal angle rounded.

DISTRIBUTION. (Fig. 32) This species is reported from Australia (King, 1853b), Philippines (Mamaril & Fernando, 1978), India (Michael & Sharma, 1988), Sri-Lanka (Rajapaksa, 1981), China (Chiang & Du, 1979), Lake Tanganyika and Venezuela (Zoppi De Roa & Vasquez, 1991), but the name *S. acutirostratus* has been so often misused for other species that its range needs to be redefined. It occurs with certainty in Australia and South-East Asia.

REMARKS. This species was originally described as a variety of *S. elizabethae*. The types are obviously lost. The original description and illustration (King, 1853b), allow identification of this remarkable species with certainty. Sars (1896) gives *S. acutirostartus* the rank of a species.

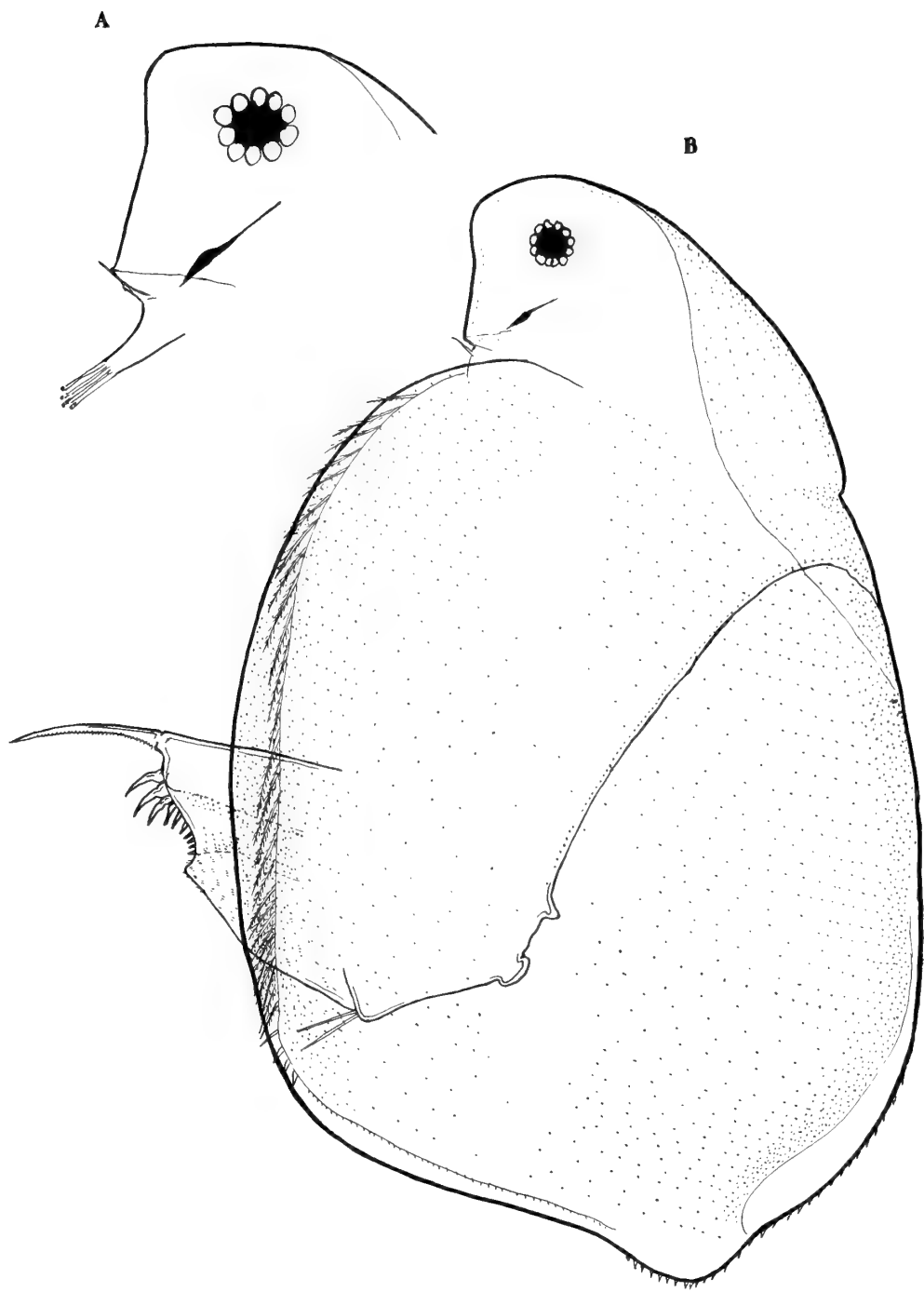


Fig. 27 *S. elizabethae*, parthenogenetic female. A, head, B, lateral view.

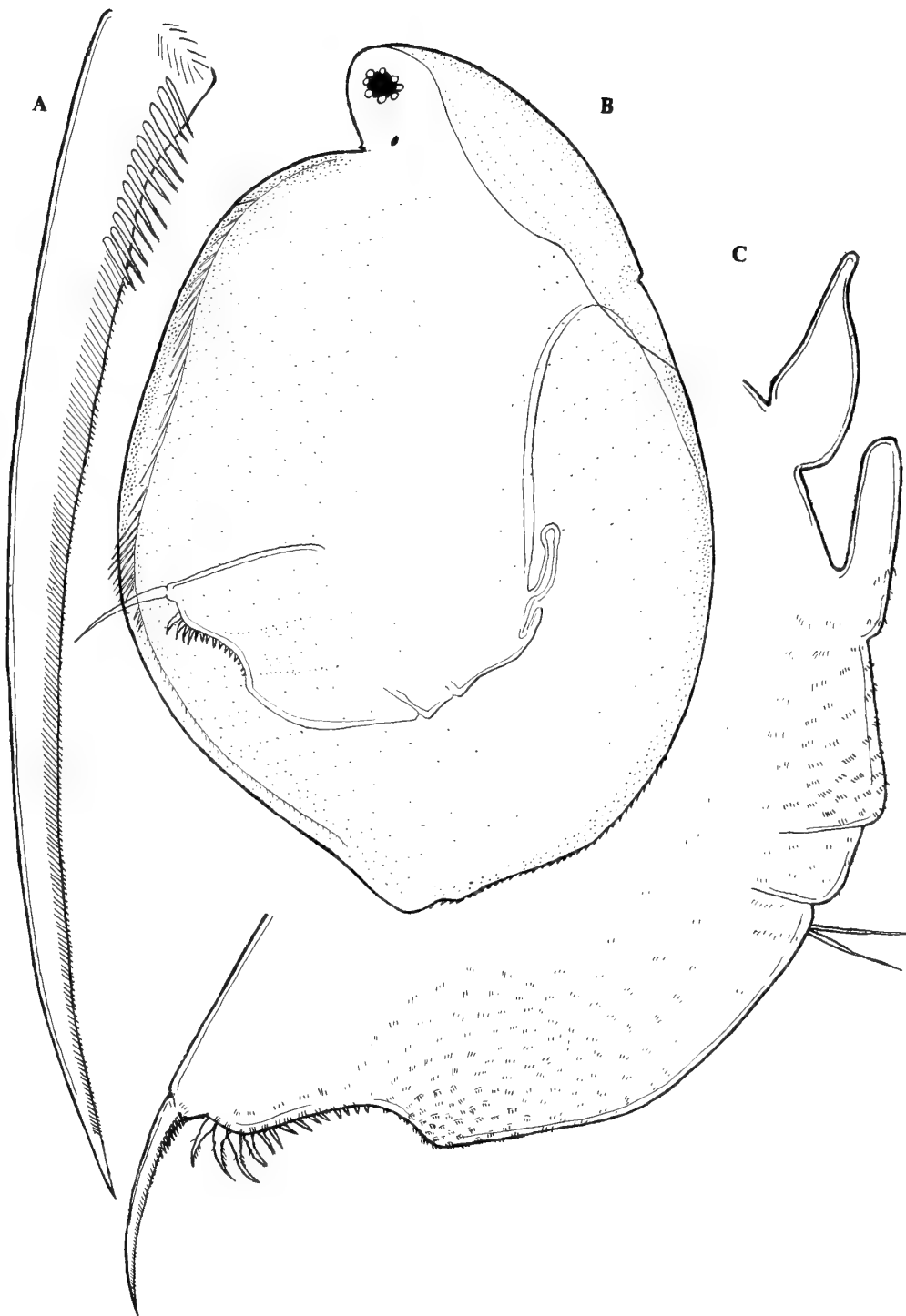


Fig. 28 *S. exspinosus*, parthenogenetic female. A, postabdominal claw, B, lateral view, C, postabdomen.

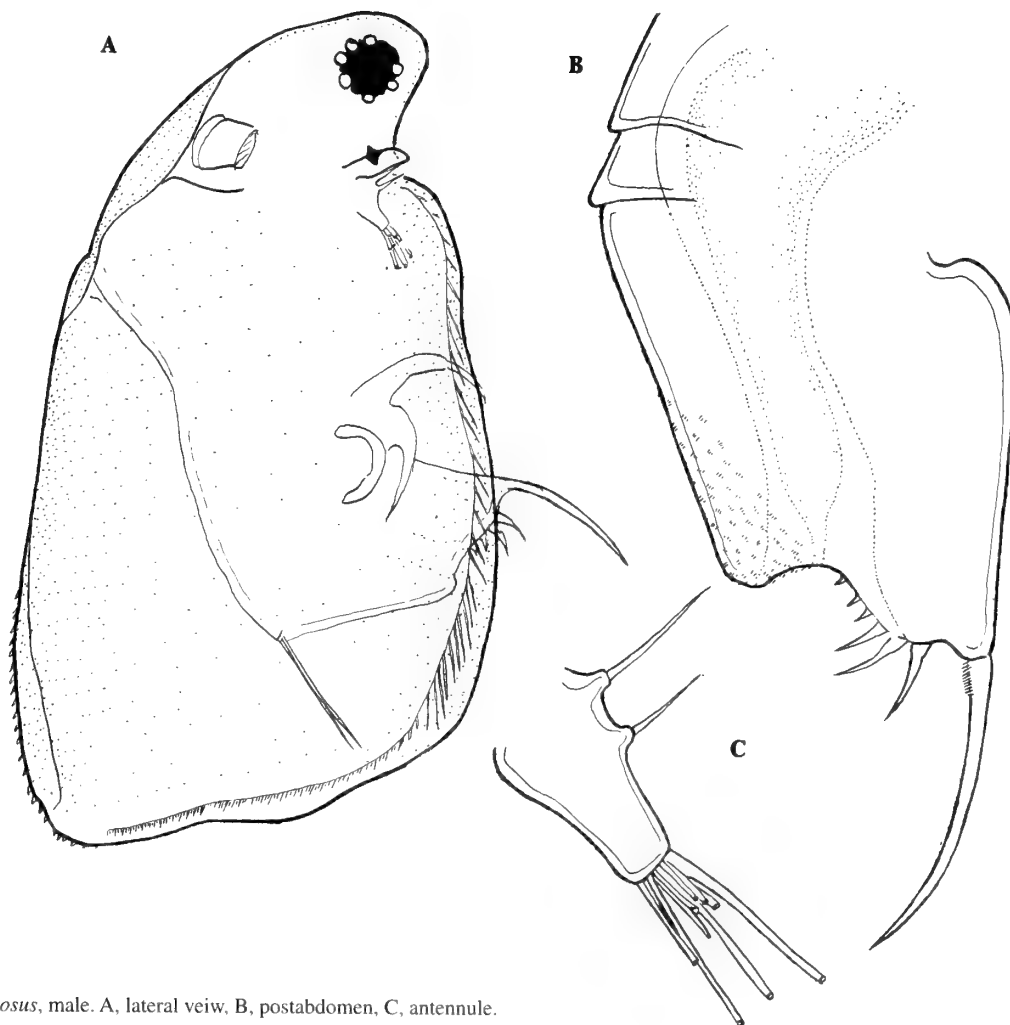


Fig. 29 *S. exspinosus*, male. A, lateral view, B, postabdomen, C, antennule.

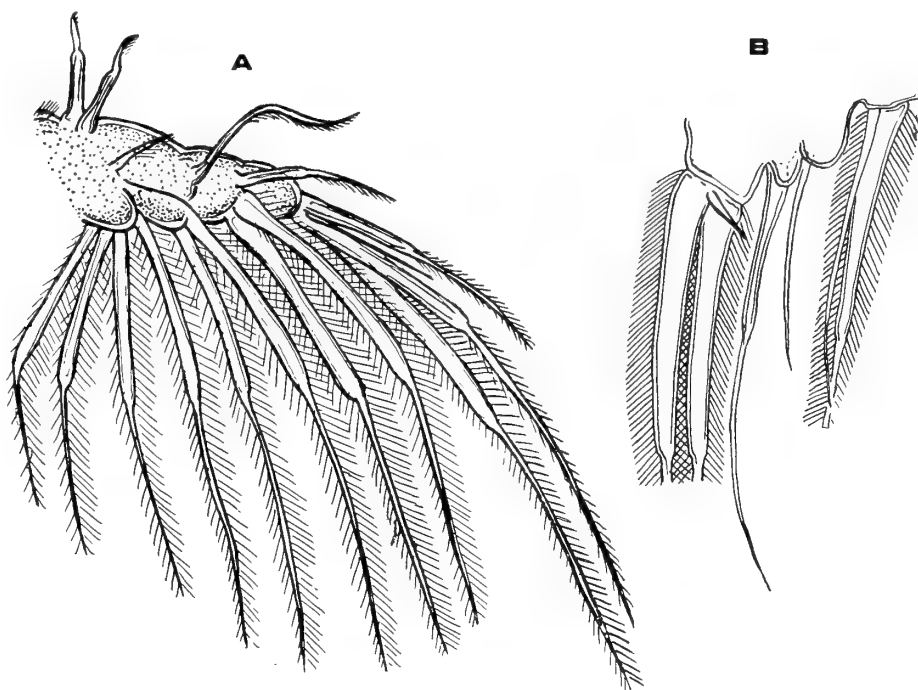


Fig. 30 *S. exspinosus* female, trunk limbs, A, 1st limb, B, endite of 2nd limb.

Schödler (1877) renamed *S. acutirostratus* as *S. paradoxus*. Consequently, the latter name is an objective junior synonym of the former.

S. vidyae Rane and *S. vidyae gajareae* Rane were described from Jabalpur (India). The descriptions (Rane, 1983, 1986) are very detailed and provided with excellent illustrations, but do not contain any characters which differentiate these taxa from *S. acutirostratus*. The types are deposited in the National collection of the Zoological Survey of India (Calcutta). Sharma & Sharma (1990) sink both names into the synonymy of *S. acutirostratus* on the basis of investigation of these types.

S. victoriensis Dumont, 1983

Fig. 36

Simocephalus acutirostratus: Haase, 1903: 150 (partim); *S. victoriensis* Dumont, 1983: 105.

TYPE MATERIAL. Holotype: Australia, Victoria, temporary pool 7km W of Edenkope, 37°2'S 141°17'E, 19. 10. 1978, leg. Morton: PVAS: ♀ ad. (AM, P31316).

MATERIAL EXAMINED. (Fig. 32) Holotype and other specimens:

Australia, New South Wales, a lake near Cooma, 12. 5. 1975: 4 ♀ ♀ ad., 12 ♀ ♀ juv. Lake Maffa, 13. 5. 1975: 3 ♀ ♀ ad., 10 ♀ ♀ juv. South Australia, Tatiara, 4km N of Bordertown, 6. 11. 1979, leg. Zeidler: 5 ♀ ♀ ad., ♀ juv. A lake on Nimakel-Bumbala road, 14. 5. 1975: 8 ♀ ♀ ad., 2 ♀ ♀ juv. The material is in SAM and AC.

DIAGNOSIS. Measurements. ♀ ♀ ad.: 1.0–3.0mm.

Female (Fig. 36). General body shape rounded. Frons with small rounde prominence separated above and below with depressions. Dorso-posterior valve prominence absent. Diameter of circle inscribed in dorso-posterior valve angle very large. Dorsal margin without denticles. Proximal and distal supra-anal angles small, embayments of postabdomen shallow, proximal angle rounded.

DISTRIBUTION. (Fig. 32) Australia: New South Wales, South Australia, Victoria.

REMARKS. There is no doubt that *S. victoriensis* and *S. acutirostratus* are separate species because they are sympatric and differ markedly from each other.

Judging from illustration made by Haase (1903), the author examined specimens of *S. victoriensis* but erroneously identified them as *S. acutirostratus*.

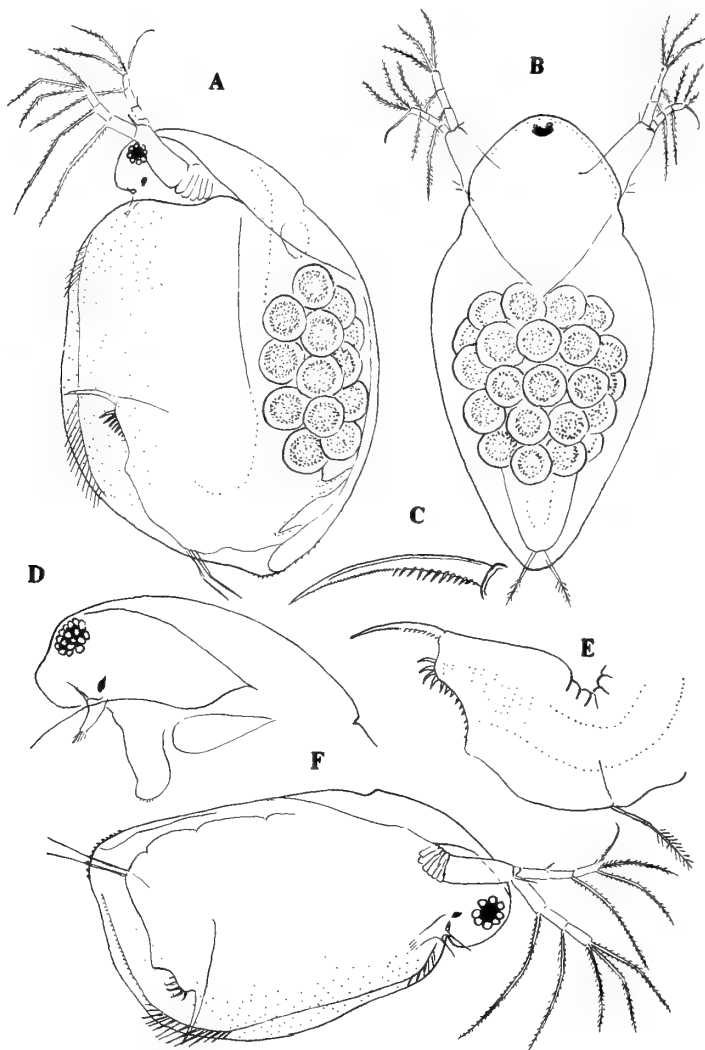


Fig. 31 *S. obtusatus* (after Sars, 1894). A, parthenogenetic female, lateral view, B, parthenogenetic female, dorsal view, C, postabdominal claw, D, head, E, postabdomen, F, male.

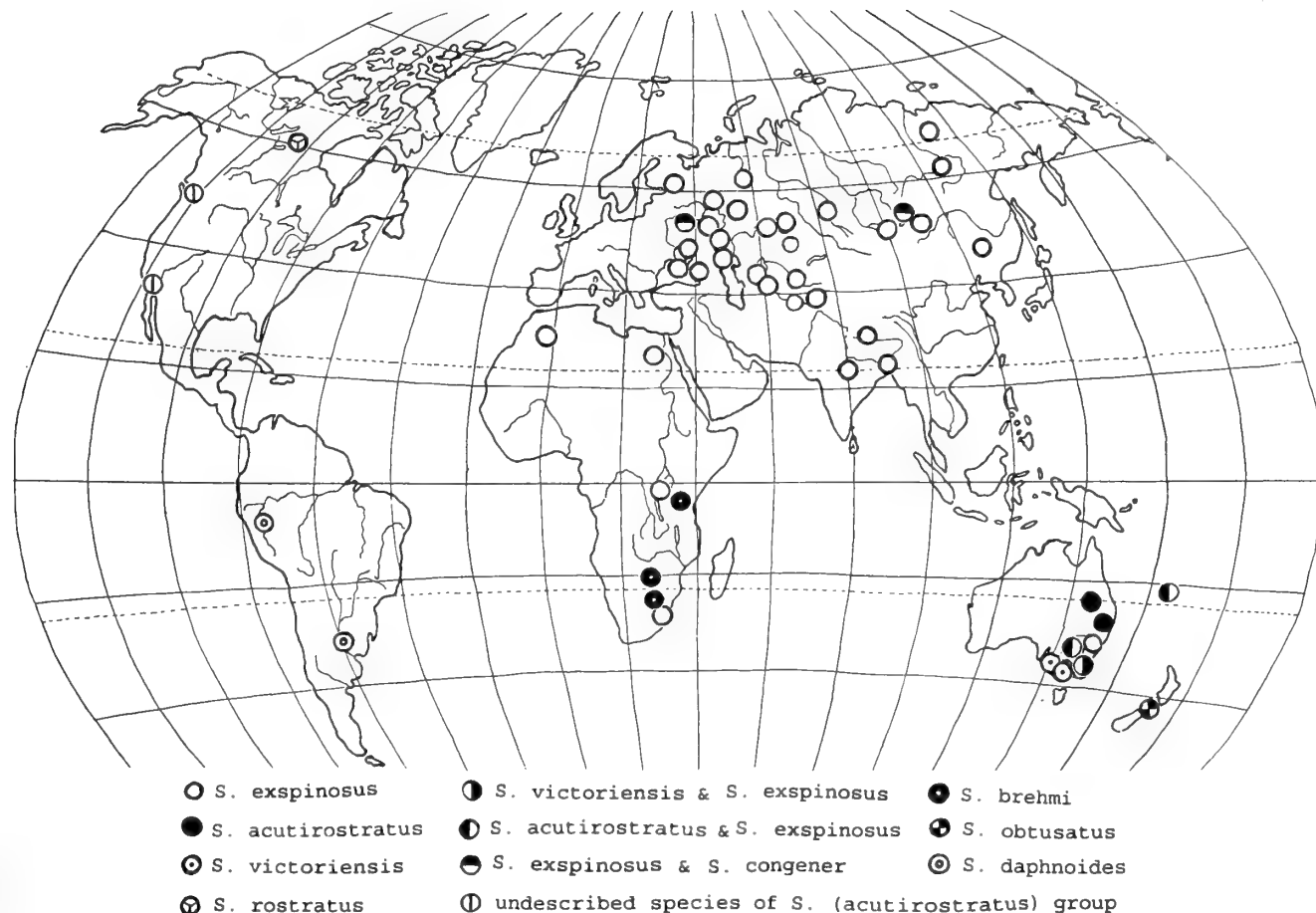


Fig. 32 Locations, where studied material of *S. (Echinocaudus)* was collected.

***S. brehmi* Gauthier, 1939 stat. nov.**

Fig. 37

Simosa acutirostrata brehmi Gauthier, 1939: 144; *Simocephalus acutifrons* Johnson, 1954: 954 syn. nov.

TYPE MATERIAL. Types (5 ♀ ad.) were in Gauthier's collection before it was nationalized by the Algerian government. There is no information about the place, where this collection is now (Hudec, 1993).

MATERIAL EXAMINED. (Fig. 32) Type material of junior synonym *S. acutifrons* Johnson. Holotype: South Africa, Kempton Park, Johannesburg: MPA: ♀ ad. (BMNH). Paratype collected with holotype: MPA: ♀ ad. (BMNH). Other specimens: Tanzania, Mt Hanang: 23 ♀ ad., 2 ♀ juv. (MCA). Southern Rhodesia, Plumtree, 7. 2. 1954: 4 ♀ ad., ♀ e., 2 ♀ juv. (ZICC).

DIAGNOSIS. Measurements. ♀ ad.: 1.0–3.0mm.

Female (Fig. 37). General body shape ovoid. Frons with small obtuse prominence not separated above and below by depressions. Dorso-posterior valve prominence distinct, separated above and below by deep, wide depressions. Diameter of circle inscribed in it moderate. Dorsal margin with denticles. Proximal and distal supra-anal angles large, embayments of postabdomen deep, proximal angle sharp.

DISTRIBUTION. (Fig. 32) Vicinity of Lake Chad, Southern Rhode-

sia, Tanzania, South Africa. This species is also reported from Brasil by Brehm (Gauthier, 1939). Unfortunately, no specimen of this species group from South America is available and it is impossible to confirm or to disprove this report.

REMARKS. *S. brehmi* differs from *S. acutirostratus* in the shape of the valves and postabdomen. These forms are allopatric, so the question of specific or subspecific rank of *S. brehmi* is difficult, but I take *S. brehmi* to be a separate species because the differences between it and *S. acutirostratus* are not less than those between other species in this group.

S. acutifrons, described from Johannesburg (South Africa), is identical to *S. brehmi*, judging by the examined type material. Johnson (1954) does not point out any characters which distinguish his species from *S. brehmi* and *S. acutirostratus*.

***S. rostratus* Herrick, 1884**

Fig. 38

Simocephalus rostratus Herrick, 1884.

TYPE MATERIAL. The type is probably lost, like those of other species described by Herrick (D. Frey, personal communication through N.N. Smirnov).

MATERIAL EXAMINED. (Fig. 32) Canada, Waterloo National Park, 15. 9. 1972, leg. Smirnov: 10 ♀ ad., 10 ♀ juv. (AC).

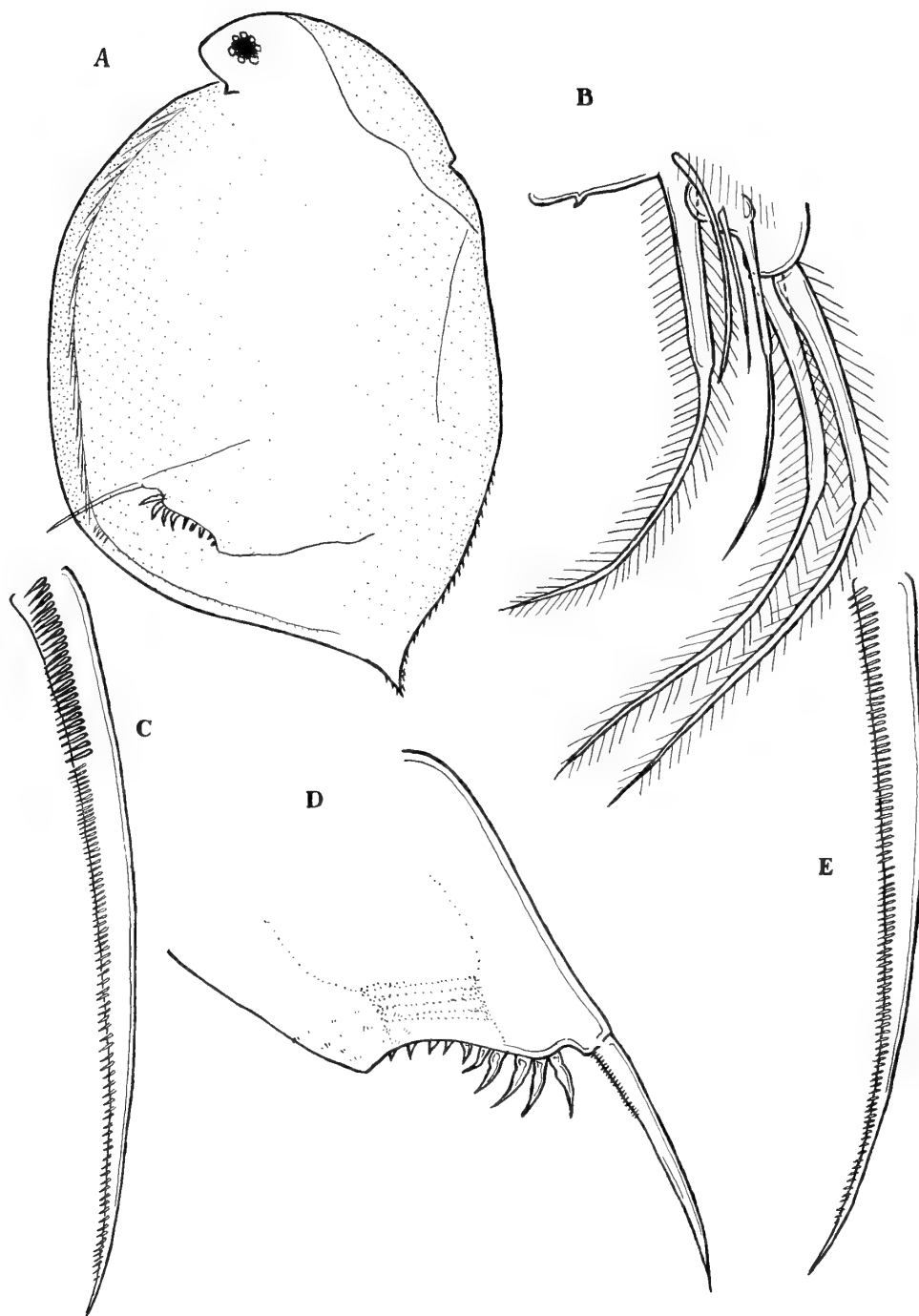


Fig. 33 *S. daphnoides*, parthenogenetic female. A, lateral view, B, endite of 2nd trunk limb, C, outer side of postabdominal claw, D, postabdomen, E, inner side of postabdominal claw.

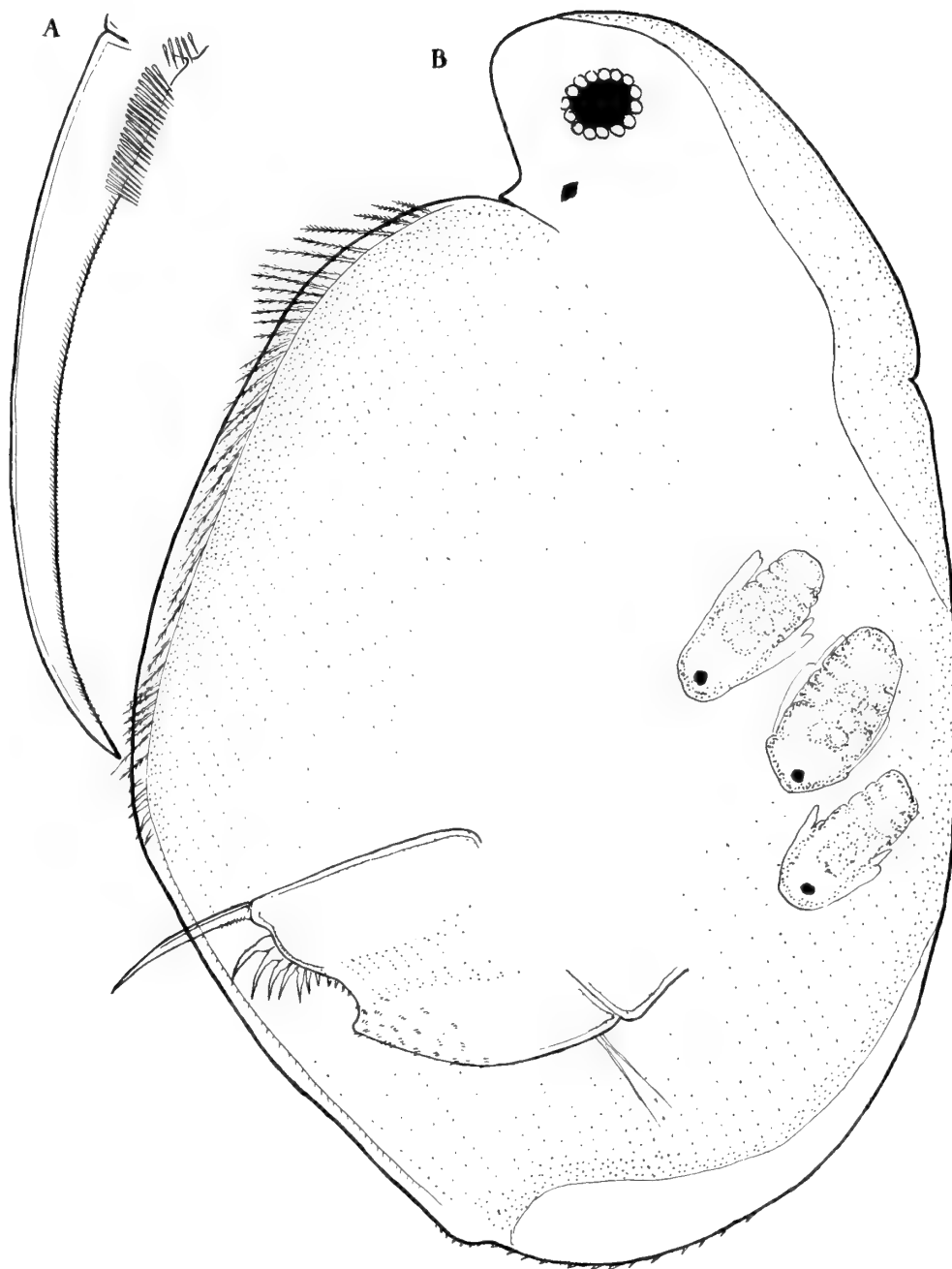


Fig. 34 *S. congener*, parthenogenetic female. A, postabdominal claw, B, lateral view.

DIAGNOSIS. Measurements. ♀ ♀ ad.: 1.0–3.0mm. Female (Fig. 38). General body shape ovoid. Frons with small obtuse prominence not separated above and below by depressions. Dorso-posterior valve prominence distinct, separated above and below by deep depressions. Dorsal margin with denticles. Diameter of circle inscribed in it small. Proximal and distal supra-anal angles small, embayments of postabdomen shallow, proximal angle rounded.

DISTRIBUTION. (Fig. 32) U.S.A., Canada.

REMARKS. The original description of this species is not provided with an illustration (Herrick, 1884). It is evident from the description that it is closely related with *S. acutirostratus*. 'The spine is as

in *S. americanus*' (*S. serrulatus*) and 'the head is produced below the eyes in an angle, like a right angle, which is not spiny'. I had serious doubt about the taxonomical state of this taxon (Orlova-Bienkowskaja, 1993), because there were no other records of *S. (acutirostratus)* species group from North America. The examination of specimens from Canada has shown that they belong to this group and differ from *S. acutirostratus*, *S. victoriensis* and *S. brehmi* in the shape of the dorso-posterior valve angle. Obviously, they belong to *S. rostratus*.

There is one undescribed species of *S. (acutirostratus)* group in North America. I have about forty specimens of this species from California and Washington, but I do not name this new species

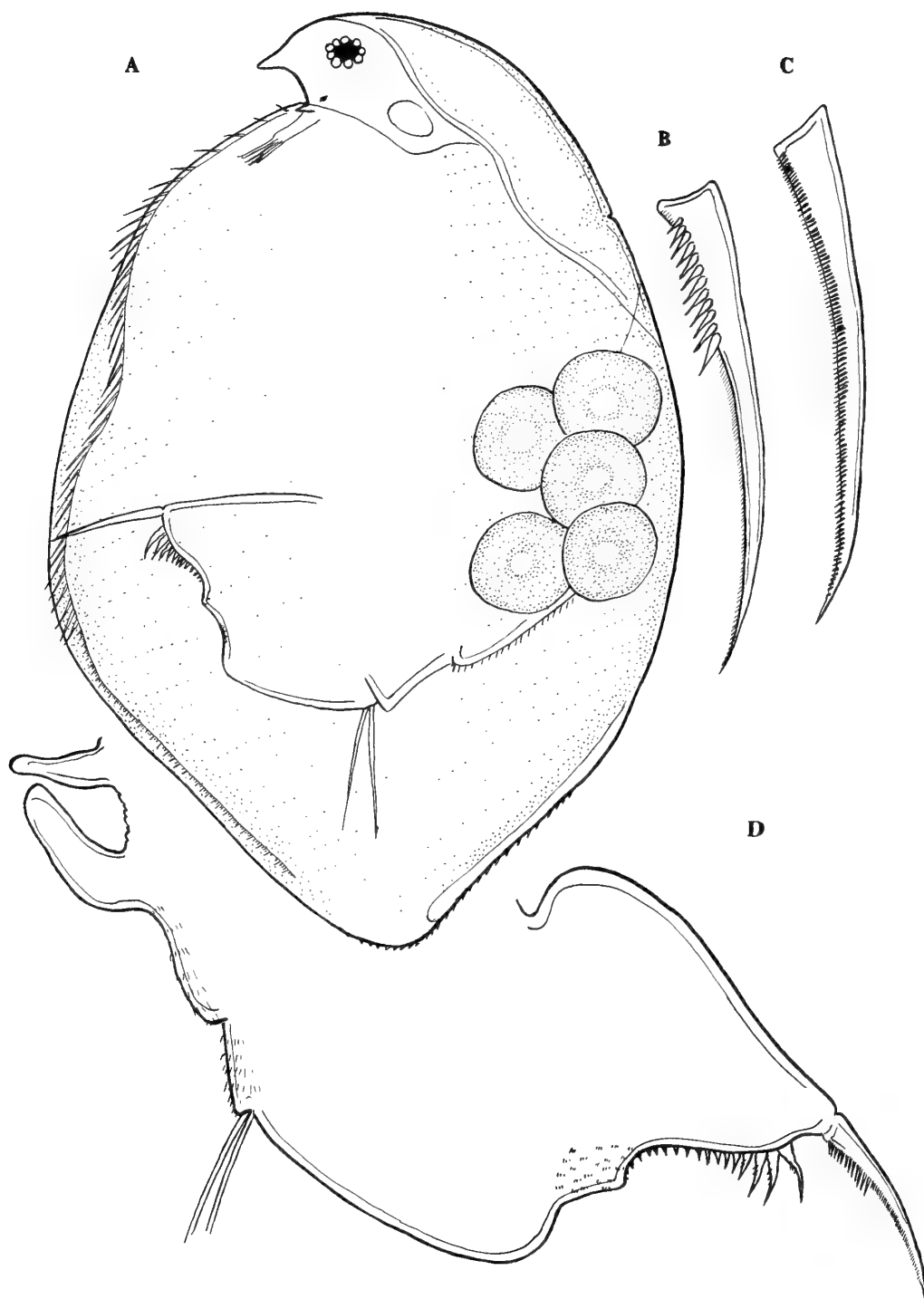


Fig. 35 *S. acutirostratus*, parthenogenetic female. A, lateral view, B, outer side of postabdominal claw, C, inner side of postabdominal claw, D, postabdomen and abdomen.



Fig. 36 *S. victoriensis*, parthenogenetic female. A, head, B, lateral view, C, postabdomen.

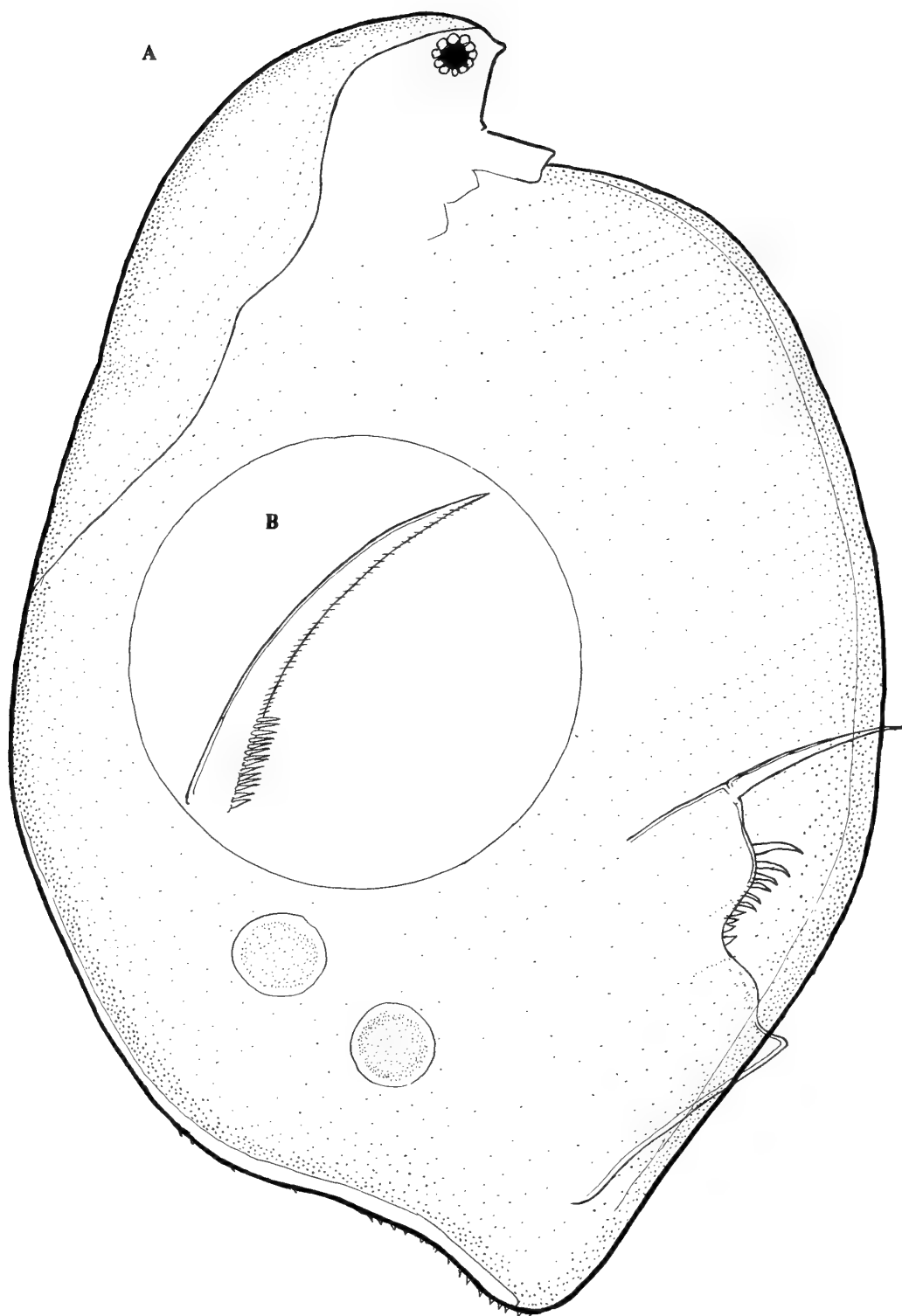


Fig. 37 *S. brehmi*, parthenogenetic female. Holotype of *S. acutifrons* = *S. brehmi*. A, lateral view, B, postabdominal claw.

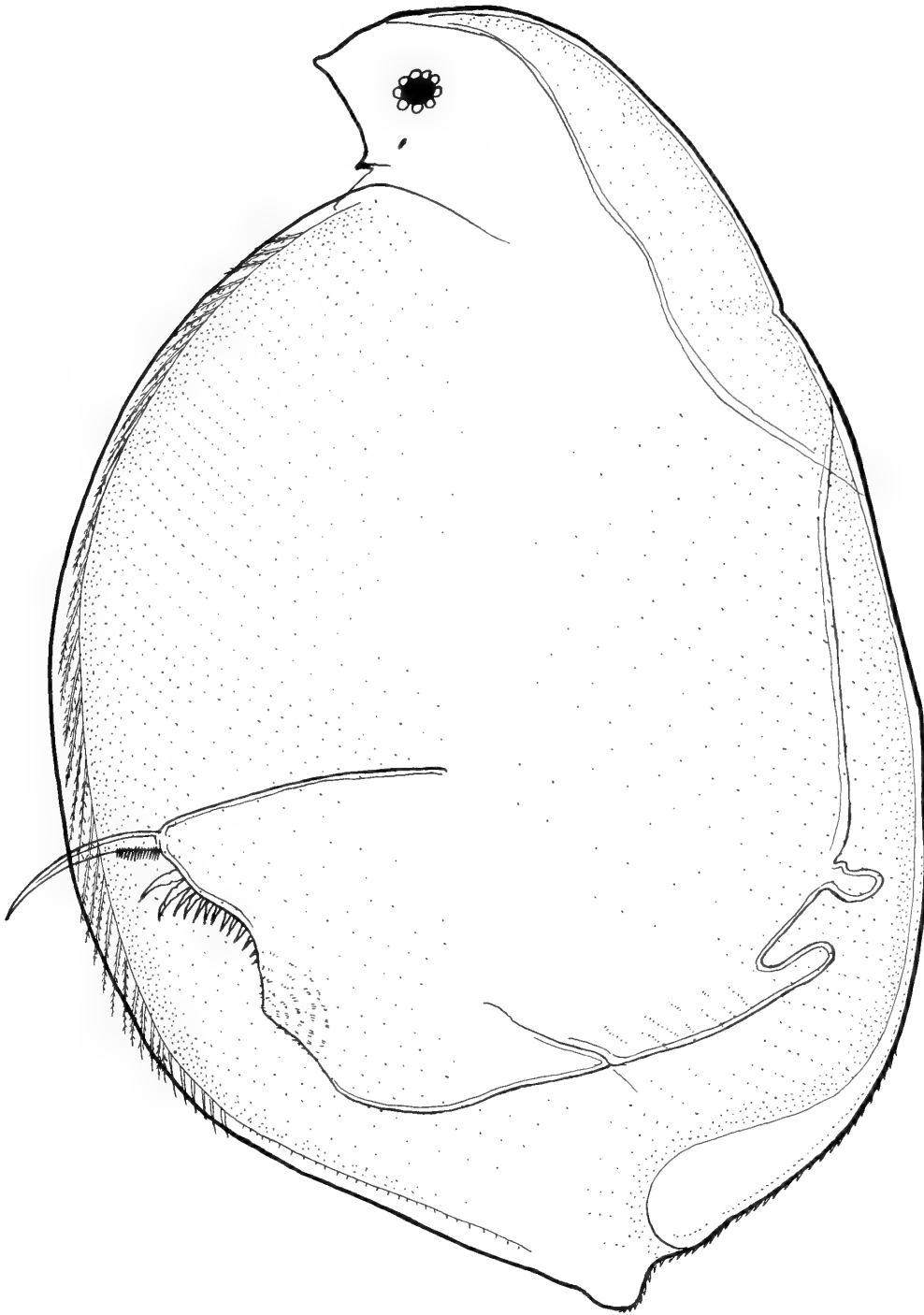


Fig. 38 *S. rostratus*, parthenogenetic female.

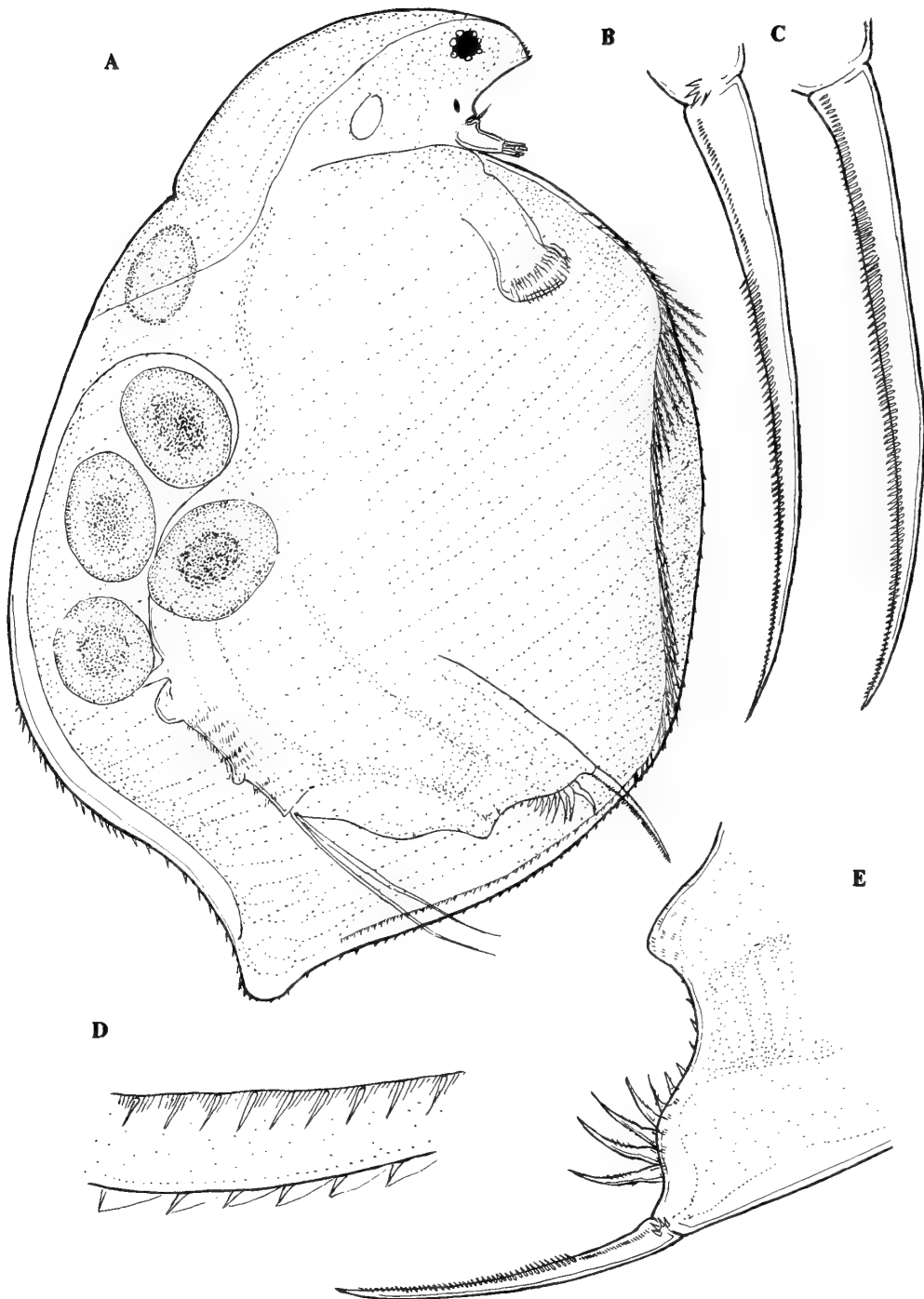


Fig. 39 *S. serrulatus*, parthenogenetic female. A, lateral view, B, outer side of postabdominal claw, C, inner side of postabdominal claw, D, setules of posterior valve margin, E, distal part of postabdomen.

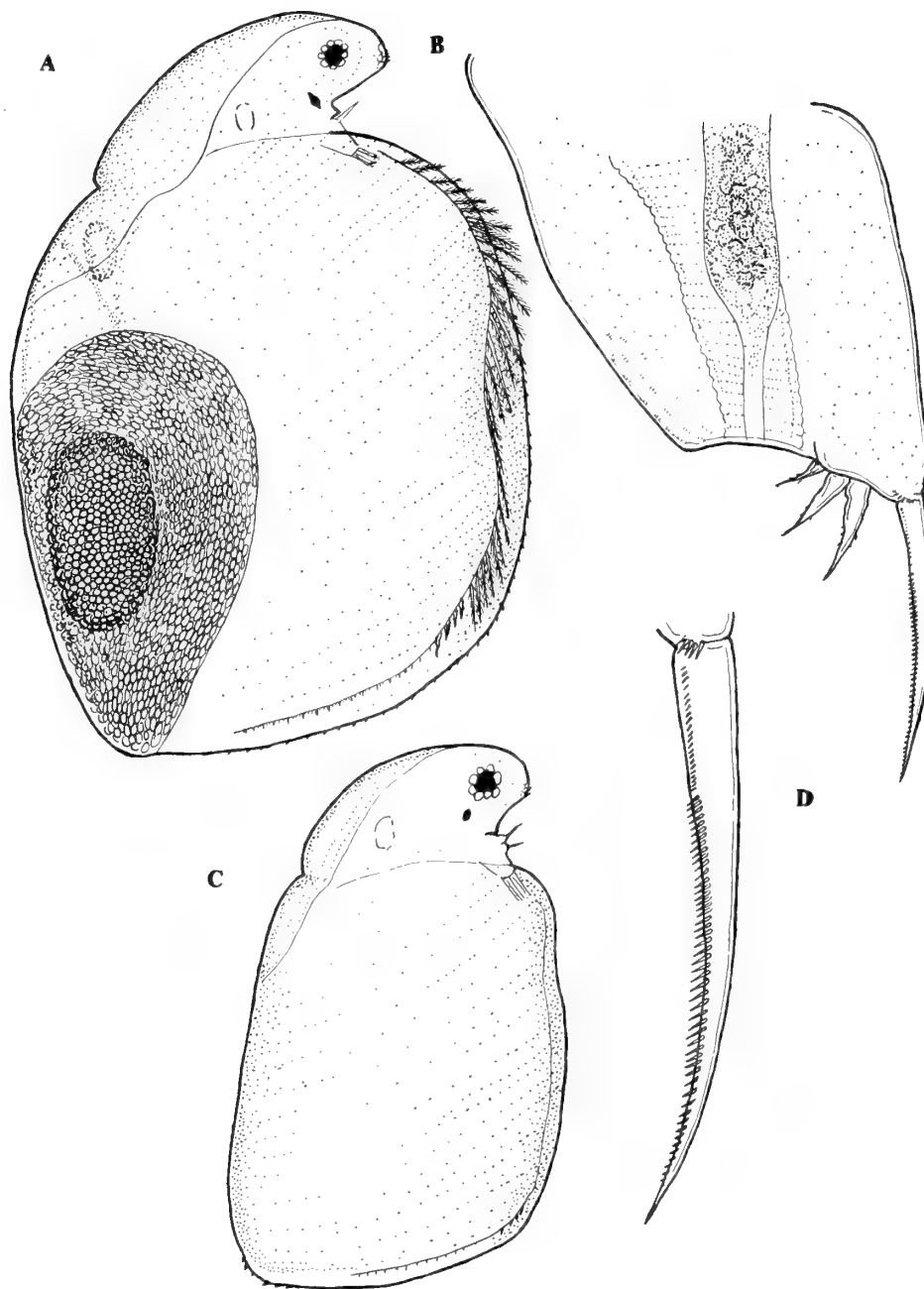


Fig. 40 *S. serrulatus*. A, ehippial female, B, postabdomen, male, C, male, D, outer side of male postabdominal claw.

because it was originally discovered by B. Hann (D. Berner, personal communication) and she has already started working on its description.

This species undoubtedly belongs to the *S. acutirostratus* species group because its frons is pointed, without denticles, and its postabdomen has two supra-anal angles. It differs from *S. acutirostratus*, *S. brehmi* and *S. rostratus* in the absence of a dorso-posterior valve prominence and from *S. victoriensis* in the shape of the postabdomen and head.

Subgenus *S. (Coronocephalus)* Orlova-Bienkowskaja, 1995

TYPE SPECIES. *Simocephalus serrulatus* (Koch, 1841).

DIAGNOSIS. Both sexes (Figs 39–42). Frons right-angled, with denticles (*S. serrulatus*, *S. semiserratus*) or without them (*S. mirabilis*). Head shield without depression. Head pores absent. Insertion of antennules at end of rostrum. Antennule short in correspondence with short rostrum, with transversal ridges covered with denticles on inner side. Aesthetes shorter than base of antennule. Postabdominal claw with spines on proximal part of outer side and on inner side. Basal part of outer side with fine setules. Anal bay of postabdomen narrow, rounded, with anal teeth.

Female. Dorso-posterior valve angle with rounded prominence. Valves without dorsal keel. Posterior corner of ehippium without protuberance. Ocellus short (*S. serrulatus* and *S. semiserratus*), or elongate (*S. mirabilis*). Setae of 2nd and 3rd endite prominence of

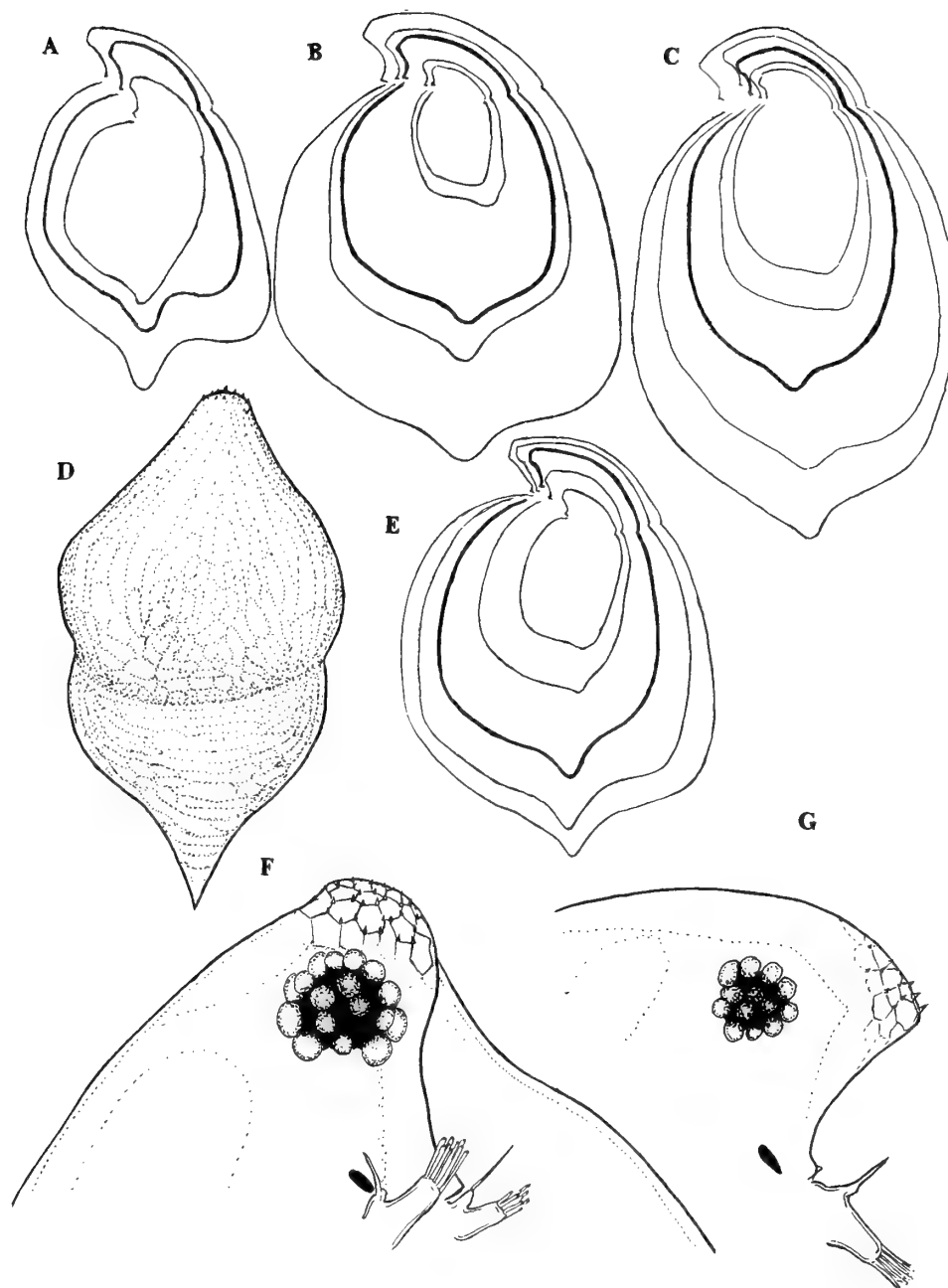


Fig. 41 *S. serrulatus*, parthenogenetic female. A – C, E, interpopulational and age variability, A, type series of *S. serrulatus* var. *montenegrinus* (Montenegro), B, series from the vicinity of Vladivostok, C, type series of *S. capensis*, E, series from Taimyr, D, head shield, dorsal, F – head, ventral, G, head, lateral.

2nd trunk limb as long as 0.3 and 0.9 or 0.6 and 0.4 of basal segment of plumose seta of 1st prominence respectively. Postabdomen with 9–15 anal teeth on each side. Supra-anal angle rounded.

Male. Supra-anal angle rounded. Vas deferens opening in middle of anal bay. Postabdomen with 3–5 anal teeth on each side. Dorso-posterior valve angle with small rounded prominence. There is no morphological hiatus between males of *S. serrulatus* and *S. semiserratus*. The male of *S. mirabilis* is unknown, so only the females of these species are described.

ETYMOLOGY. The name '*Coronocephalus*' is derived from the words '*corona*' – 'crown' and '*cephalon*' – 'head' and refers to spines on the head that are typical of this subgenus.

REMARKS. The subgenus consists of three species: *S. serrulatus*, *S. semiserratus* and *S. mirabilis* sp.nov. The first is distributed world-wide. Statistical analysis of its variation (Orlova-Bienkowskaja, 1995a) has revealed that it has no geographical races and that there is a morphological hiatus between *S. serrulatus* and *S. semiserratus* in two pairs of independent metric characters. In addition, these species differ from each other in the number of denticles on the valve margin. *S. serrulatus* and *S. semiserratus* are sympatric in South America. Therefore, they are not subspecies but separate species. *S. mirabilis* differ from *S. serrulatus* and *S. semiserratus* in having an elongate ocellus and in the absence of denticles on the frons.

***S. serrulatus* (Koch, 1841)**

Figs 39–42

Daphnia serrulata Koch, 1841: 35; *D. brandtii* Fischer, 1848: 177; *D. intermedia* Lievin, 1848: 29; *Simocephalus serrulatus*: Schödler, 1858; *Simocephalus americanus* Birge, 1878; *S. capensis* Sars, 1895: 15; *S. inflatus* Vávra, 1900: 12; *S. serrulatus* var. *productifrons* Stingelin, 1904: 57; *S. serrulatus* var. *montenegrinus* Werestchagin, 1912: 7; *S. serrulatus* var. *mixta* Grochmalicki, 1915: 220 (nec *S. mixtus* Sars, 1903); *S. serrulatus* var. *rotundifrons* Brehm, 1933: 54; *S. kerhervei* Bergamin, 1939: 63; *S. aqua-brankai* Bergamin, 1939: 64; *S. serrulatus* var. *armata* Brehm, 1956: 221; *S. serrulatus* var. *pelagicus* Brehm, 1959; *S. surekhae* Rane, 1985a: 159.

TYPE MATERIAL. The types appear to be lost. No type locality is indicated in the original description. Probably it is in Germany.

MATERIAL EXAMINED. (Fig. 43) Type material of junior synonyms: *S. serrulatus montenegrinus* Werestchagin, 1912: Lectotype (designated by Orlova-Bienkowskaja (1995a)): Montenegro, Lake Scutari, 15. 6. 1911, leg. Werestchagin : MPA: ♀ ad. (ZICC, 7085). Paralectotypes collected with lectotype: MPA: 3 ♀ ad., ♀ juv (ZICC, 7085, 7086), Montenegro, vicinity of Rijeka, leg. Werestchagin: CBS: 2 ♀ ad., 2 ♀ juv. (ZICW). *S. capensis* Sars, 1895: Lectotype (designated by Orlova-Bienkowskaja (1995a)):

SouthAfrica, Knysna, hatched from dry epphipia: MPA: ♀ ad. (ZMO, F 18357). Paralectotypes collected with lectotype: MPA: 15 ♀ ad., 10 ♀ juv., 8 ♀ e. (ZMO, F 18357), 16 ♂♂ (ZMO, F 183578). Other specimens: about 1500 specimens (♀ ad., ♀ juv., ♀ e. and ♂♂) from Russia, Kazakhstan, China, India, Bangladesh, Vietnam, Burkina Faso, Central Africa, Niger, Nigeria, Mauritania, Sudan, Canada, U.S.A., Guatemala, Nicaragua, Argentina, Brasil, Australia (ZICW, ZIPD, AM, AC). More precise geographical data have been published previously (Orlova-Bienkowskaja, 1995a).

DIAGNOSIS. Measurements. ♀ ad.: 1.0–2.0mm, ♀ e. 1.0–1.5mm, ♂♂: 0.7–1.0mm.

Female. Dorso-posterior valve prominence large, separated from the rest of valves by deep embayment. Its length exceeds the diameter of a circle inscribed in its contour. Denticles cover the ventral, posterior and more than 1/3 of the dorsal margin. Ocellus short. Frons with denticles. Setae of 2nd and 3rd endite prominence of 2nd trunk limb as long as 0.3 and 0.9 of the basal segment of plumose seta of 1st prominence respectively.

DISTRIBUTION. (Fig. 43) Europe, Asia, Africa, North America, South America, Australia.

REMARKS. Fig. 41 shows the interpopulational variability of head height, and size and shape of the dorso-posterior valve angle. A number of subspecies and even separate species have been described

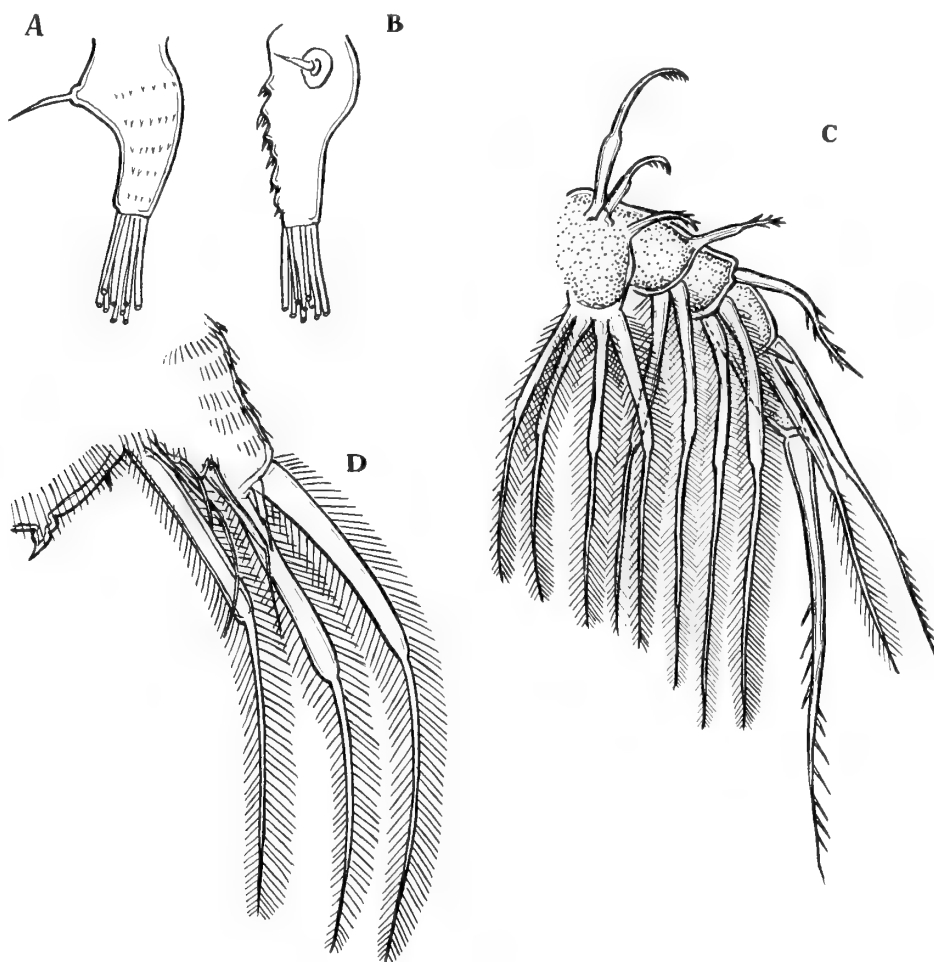


Fig. 42 *S. serrulatus*, female. A, antennule, lateral, B, antennule, dorsal, C, 1st trunk limb, D, endite of 2nd trunk limb.

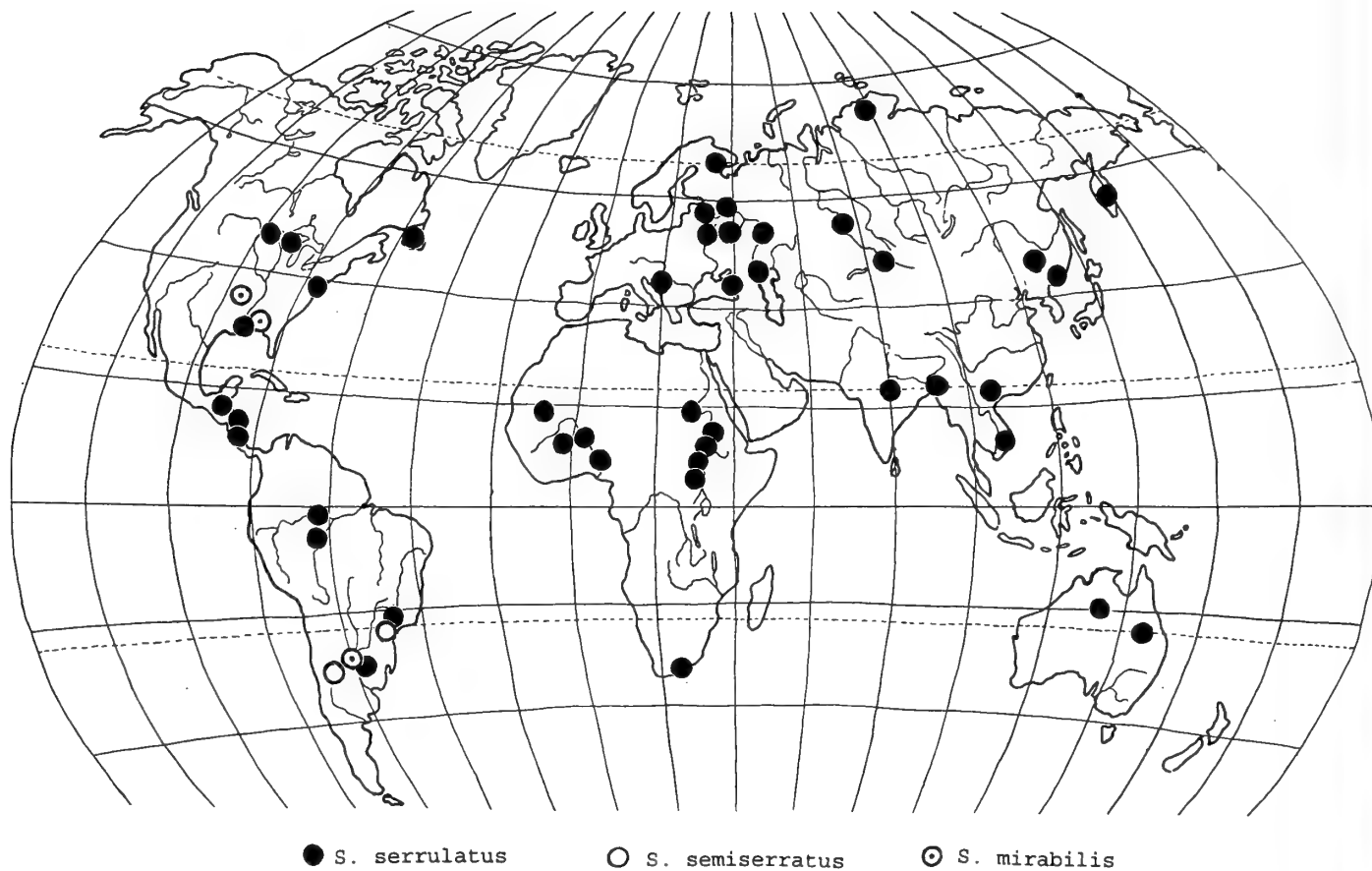


Fig. 43 Locations, where the studied material of *S. (Coronocephalus)* was collected.

because of these variations. However, I believe, that *S. serrulatus* has no subspecies. First, there is no morphological hiatus between populations. There are always some specimens with intermediate characters (Orlova-Bienkowskaja, 1995a). Second, the variability is not geographical and sometimes neighbouring populations differ more strongly than populations from different continents.

This interpopulational variability is probably the consequence of the founder-effect, which is strong in Cladocera because of parthenogenesis. It conforms with the data of Hann & Hebert (1986), who studied the genetic structure of North American *Simocephalus* populations. Based on a study of enzymes, these authors came to the conclusion that the genetic diversity within populations is less than between populations. They supposed it to be a consequence of the founder-effect.

The original description of *S. serrulatus* was supported by good illustration and contains most of the characters which differentiate this species from others (Koch, 1841).

S. brandtii and *S. intermedius*, described from Europe, are traditionally regarded as synonyms of *S. serrulatus*. The types are probably lost, but the original descriptions (Fischer, 1848; Lievin, 1848) show that this opinion is correct. The name *S. vetulus* var. *brandtii* Cosmovici, 1900 is the junior secondary homonym of *S. brandtii* (*Daphnia brandtii* Fischer, 1848). According to Article 59a of the International Code of Zoological Nomenclature (1988), it is invalid. It is not necessary to propose the replacement name (Art. 60a), because *S. vetulus* var. *brandtii* is the junior synonym of *S. vetulus*. The name *S. intermedius* Studer is not the secondary homonym of *S. intermedius* (Lievin) (*Daphnia intermedia* Lievin,

1848) (Art. 60c), because the species described by Studer (1878) is assigned to the genus *Simocephalus* erroneously and belongs to the genus *Daphnia*.

S. serrulatus var. *montenegrinus* Werestchagin, 1912 was described from Montenegro (Fig. 41A). It is regarded as a subspecies (Behning, 1941), or as a synonym of *S. serrulatus* (Šrámek-Hušek *et al.*, 1962; Negrea, 1983). Werestchagin (1912) writes that this variety differs from the typical form in the higher head and the longer dorso-posterior valve prominence. Statistical analysis of these metric characters in type specimens shows that there is no morphological hiatus between this variety and *S. serrulatus* (Orlova-Bienkowskaja, 1995a).

S. surekhae Rane is described from Jabalpur (India) (Rane, 1985a). The author does not point out any differences between this species and *S. serrulatus*. Sharma & Sharma (1990) have studied the types and sunk *S. surekhae* into the synonymy of *S. serrulatus*. This conforms with my data, because the available specimens from Jabalpur belong to the latter species.

S. serrulatus var. *rotundifrons* Brehm is also a synonym of *S. serrulatus* (Šrámek-Hušek *et al.*, 1962; Flössner, 1972). In the opinion of Brehm (1933) this variety described from Gao (Mali) differs from the typical *S. serrulatus* in its rounded head and the shorter dorso-posterior valve prominence. The types are lost (Smirnov N.N., personal communication). Statistical analysis shows that specimens available from Niger do not differ from those from Europe in these characters (Orlova-Bienkowskaja, 1995a).

S. capensis Sars was described from the vicinity of Knysna (South Africa) (Fig. 41C). Sars (1895) writes that this species is closely

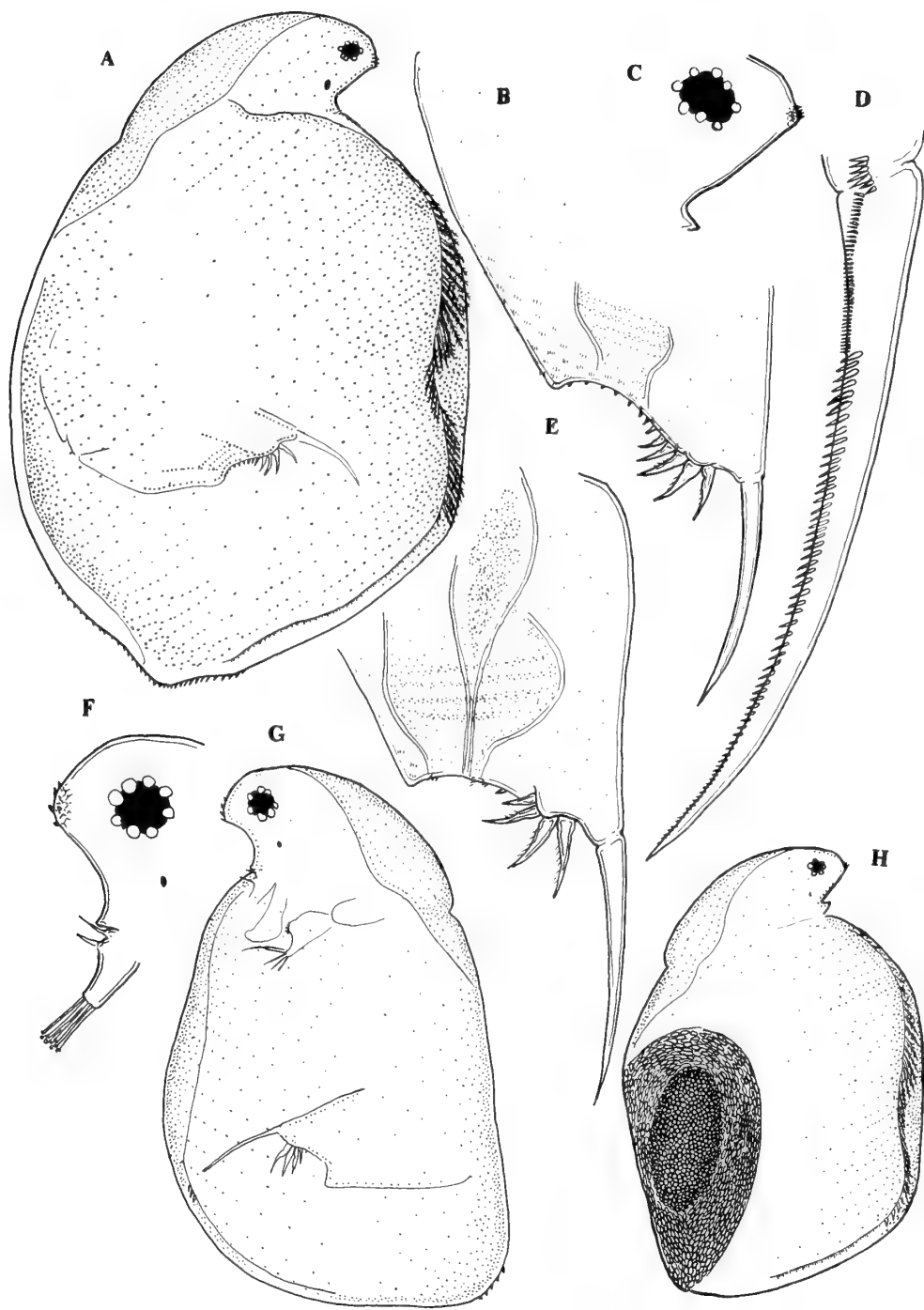


Fig. 44 *S. semiserratus*. A, parthenogenetic female, B, postabdomen, female, C, distal head part, female, D, outer side postabdominal claw, female, E, postabdomen, male, F, distal part of head, male, G, male, H, ephippial female.

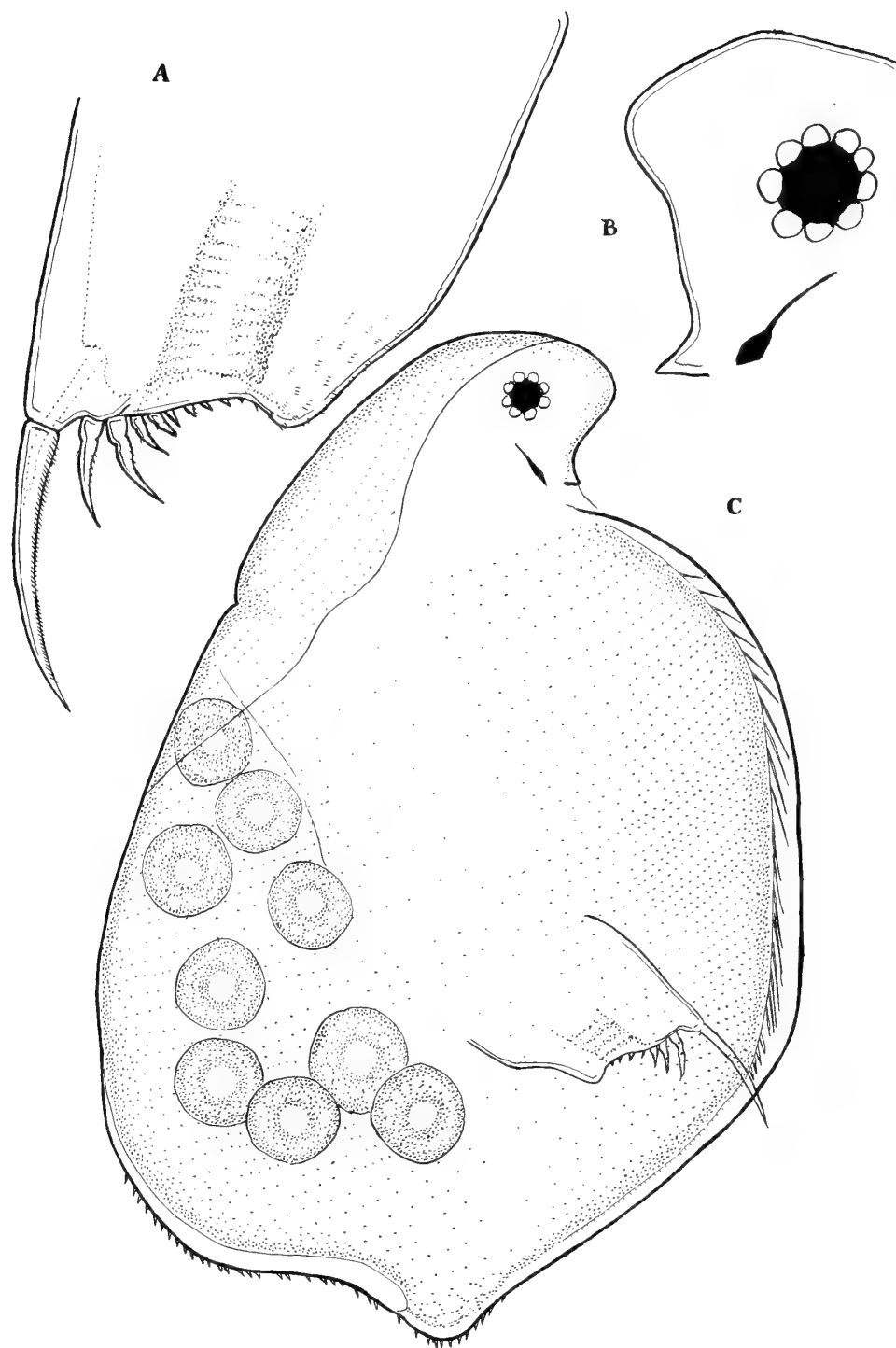


Fig. 45 *S. mirabilis* sp. nov., female. A, postabdomen, B, head, C, lateral view of holotype.

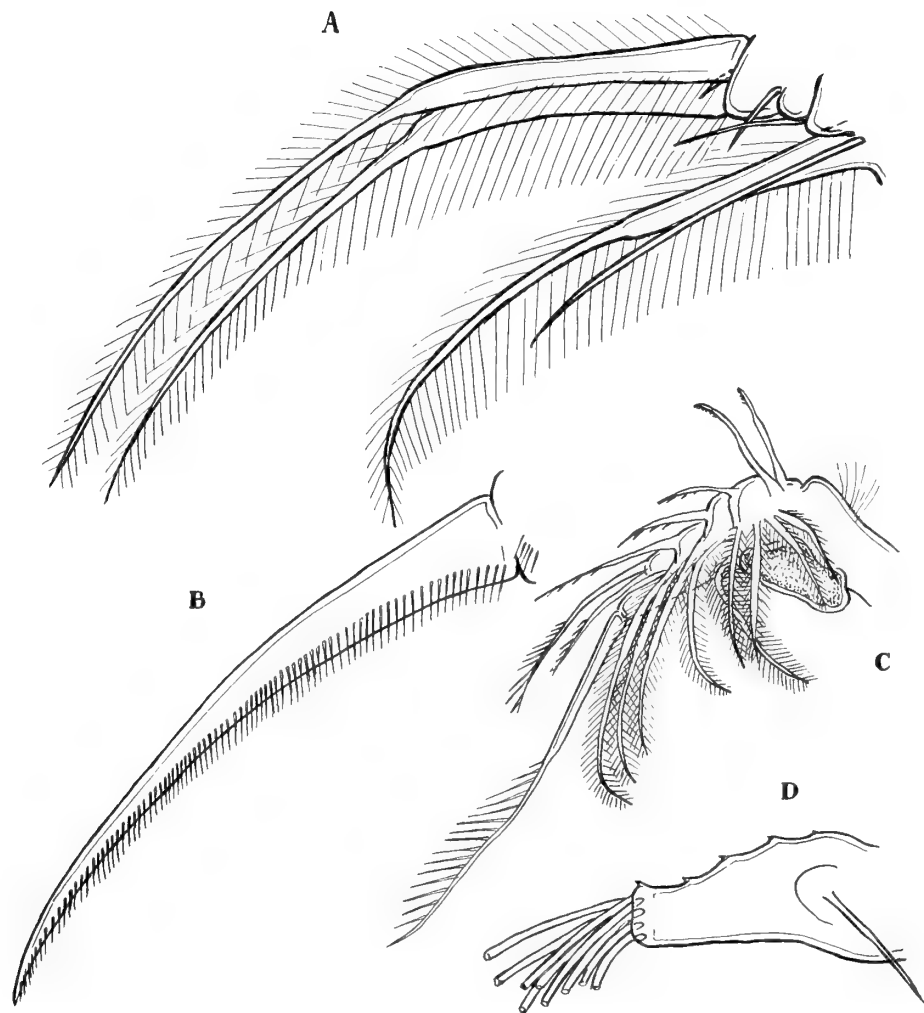


Fig. 46 *S. mirabilis* sp. nov., female. A, endite of 2nd trunk limb, B, postabdominal claw, C, 1st trunk limb, D, antennule.

related with *S. serrulatus* but differs from it in head shape and the absence of denticles on the posterior valve margin below the prominence. Analysis of the head height in the type specimens reveals that it does not differ in this respect from European specimens of *S. serrulatus* (Orlova-Bienkowskaja, 1995a). The denticles of the posterior margin are present in the types, but they are covered with a semitransparent substance. I agree with the opinion of Fryer (1957) that *S. capensis* is a synonym of *S. serrulatus*.

S. americanus Birge is described from North America. There is no information about the types and type locality. The original description (Birge, 1878) reveals that this species is closely related with *S. serrulatus*. In the opinion of Birge, it differs from the latter because it has a rhomb-like ocellus and the postabdominal claw is covered with denticles. Obviously, this is a misunderstanding because *S. serrulatus* has the same characters.

S. serrulatus var. *armata* Brehm was described from Venezuela. According to Brehm (1956), it differs from the typical form because its antennules have ridges covered with denticles. But the typical form has the same ridges and denticles, so this variety is a synonym of *S. serrulatus* (Flössner, 1972; Negrea, 1983). The illustration in the original description has the caption '*S. serrulatus* var. *barbata*'. Obviously, this is an inadvertent error.

S. inflatus Vávra was described from Valdivia (Chile) (Vávra,

1900). There is no information about the types. Vávra does not point out any differences between *S. inflatus* and *S. serrulatus*. He writes that *S. inflatus* differs from *S. capensis* in the head shape, small ocellus and general body shape. Daday (1905) supposes this name to be a synonym of *S. capensis*, because he found some specimens with intermediate characters in Paraguay. Michael & Sharma (1988) believe it to be a synonym of *S. serrulatus*. I agree with them because the original description, provided with a good illustration, contains all the important characters of the latter species.

S. kerhervei and *S. aguabrankai*, described from São Paulo (Brasil), are not mentioned in recent literature. There is no information about the types. The illustrations in the original description (Bergamin, 1939), suggest that both types are juveniles with denticles on the head and a row of denticles along the postabdominal claw. The differences between these species and *S. serrulatus* are not indicated. The available material from São Paulo does not differ from the latter species (Orlova-Bienkowskaja, 1995a). Therefore *S. kerhervei* and *S. aguabrankai* are the junior synonyms of *S. serrulatus*.

S. serrulatus var. *productifrons*, described from Sumatra (Stingelin, 1904), is also synonym of *S. serrulatus* (Šrámek-Hušek *et al.*, 1962; Negrea, 1983). The type material is lost (Frenzel, 1987). According to Stingelin (1904), this variety differs from *S. serrulatus*, *S. inflatus* and *S. americanus* by the elongate, pointed head and the large

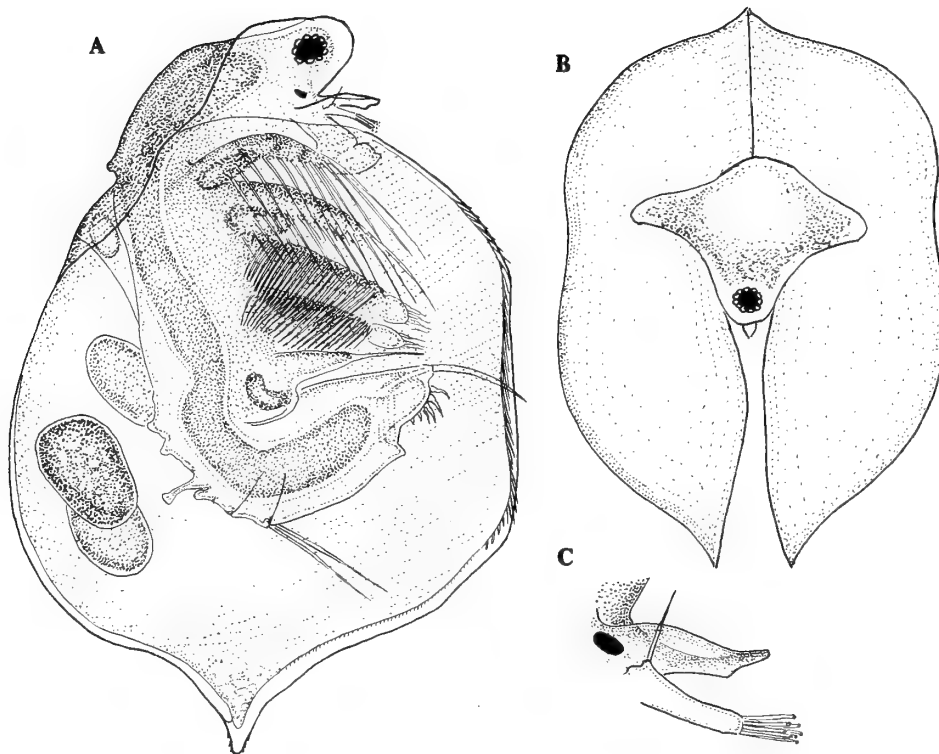


Fig. 47 *S. latirostris*, parthenogenetic female. A, lateral view, B, anterior view, C, rostrum and antennule.

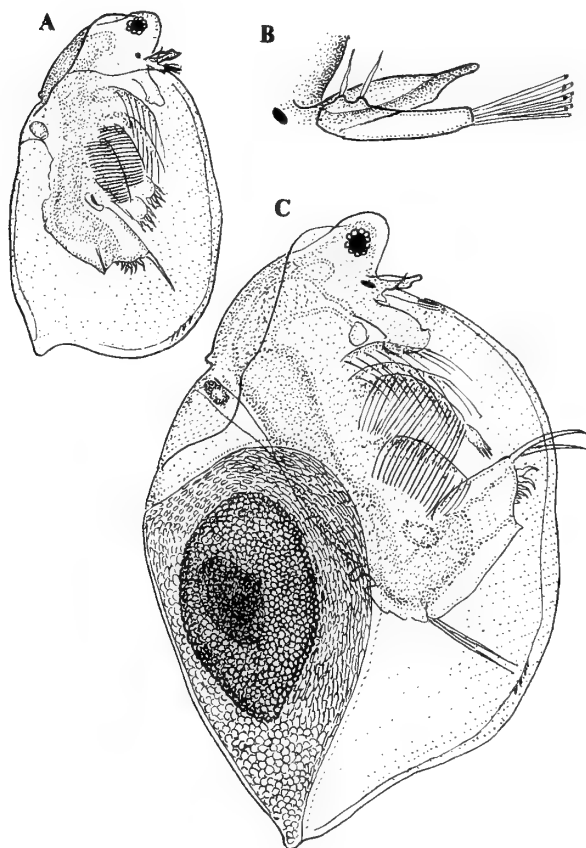


Fig. 48 *S. latirostris*. A, male, B, rostrum and antennule, male, C, ephippial female.

number of denticles. I believe that both features vary within populations and cannot be diagnostic characters.

S. serrulatus var. *mixta*, described from Java, differs from the typical *S. serrulatus* by the high head, large eye and elongate ocellus (Grochmalicki, 1915). I have no material from Java, but specimens from South-East Asia and Australia do not differ from European *S. serrulatus*. Furthermore, the diagnostic characters of this form varies within populations. I suppose this variety to be a synonym of *S. serrulatus*. In addition, *S. serrulatus* var. *mixtus* is the primary junior homonym of *S. mixtus* Sars, 1903.

S. serrulatus var. *pelagicus* Brehm was described from the pelagial zone of a small lake in New Guinea (Brehm, 1959). The type material, consisting of juvenile females, is probably lost (N.N. Smirnov, personal communication). The author does not point out any other differences between *S. serrulatus* var. *pelagicus* and typical *S. serrulatus* except the head shape. I take *S. serrulatus* var. *pelagicus* to be a synonym of *S. serrulatus*, because this character varies within populations.

'*S. serrulatus* var. *spinosulus* Stingelin, 1904' mentioned by Flössner (1972) as a synonym of *S. serrulatus*, does not exist. The variety *S. vetulus* var. *spinosulus* Stingelin belongs to the subgenus *Simocephalus* s. str.

S. semiserratus Sars, 1901

Fig. 44

Simocephalus semiserratus Sars, 1901: 23; *S. capensis* (*S. semiserratus* Sars, 1901): Daday, 1905: 209; *S. serrulatus* (*S. semiserratus* Sars, 1901): Kanduru, 1981: 72; Michael & Sharma, 1988: 83.

TYPE MATERIAL. Lectotype (designated by Orlova-Bienkowskaja (1995a)): Brasil, São Paulo, Itatiba: CBS: ♀ ad. (ZMO, F 9176).

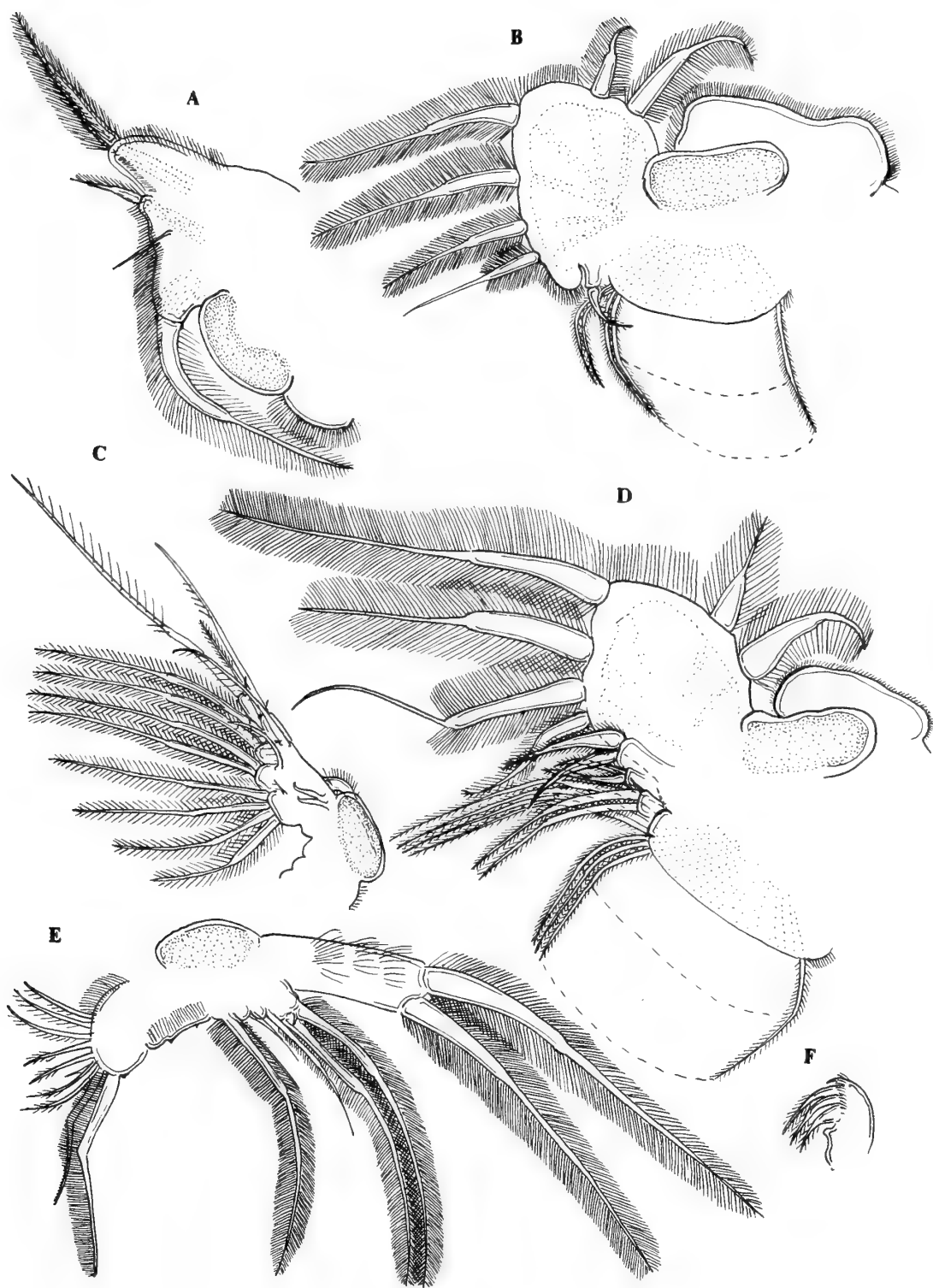


Fig. 49 *S. latirostris* appendages, female. A, 5th trunk limb, B, 4th trunk limb, C, 1st trunk limb, D, 3rd trunk limb, E, 2nd trunk limb, F, maxillule.

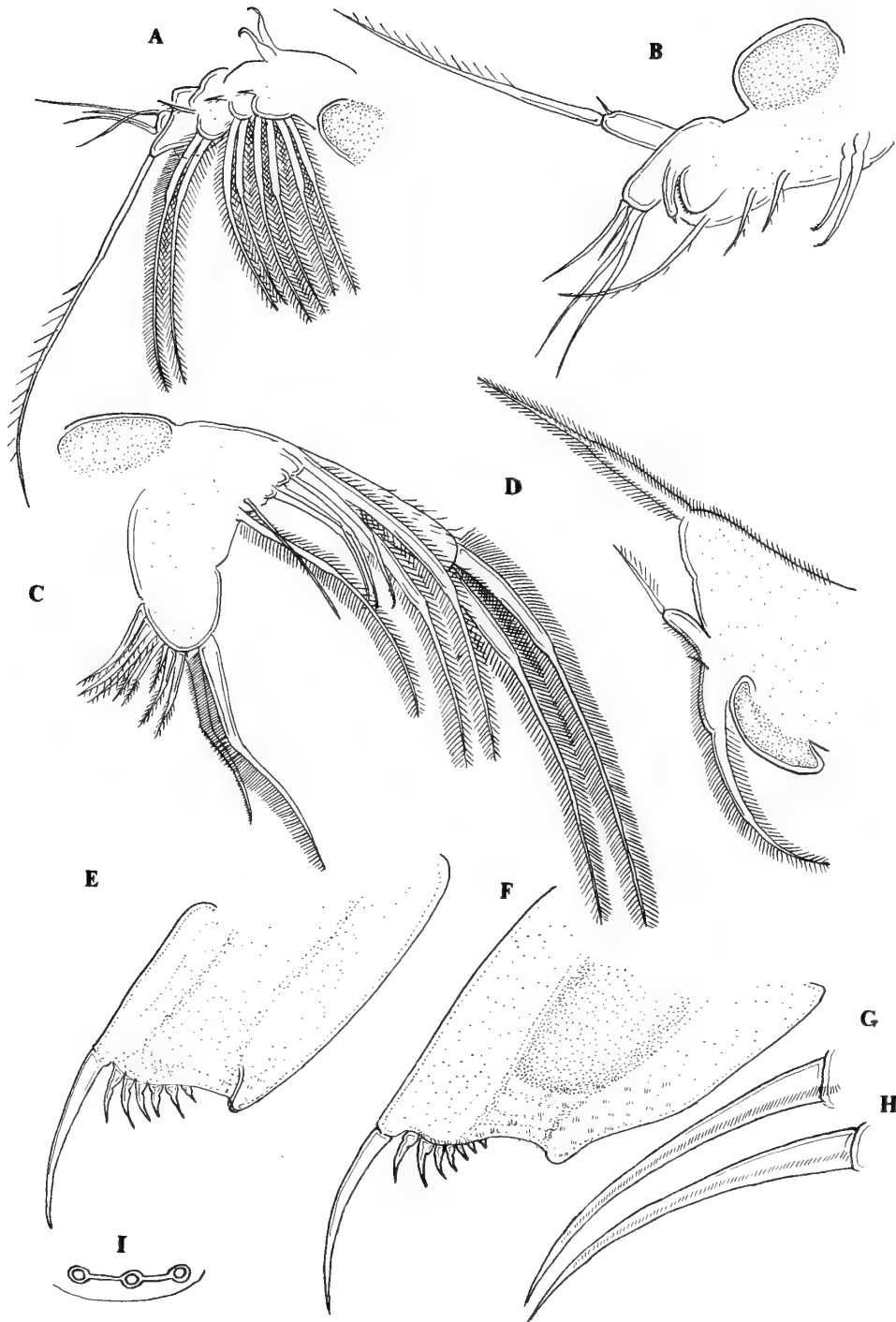


Fig. 50 *S. latirostris*. A, lateral view of 1st trunk limb, male, B, frontal view of 1st trunk limb, male, C, 2nd trunk limb, male, D, 5th trunk limb, male, E, postabdomen, male, F, postabdomen, female, G, outer side of postabdominal claw, H, inner side of postabdominal claw, I, head pores.

Paralectotypes collected with lectotype: CBS: 9 ♀ ♀ ad., 2 ♀ ♀ juv. (ZMO, F 9176, F 9177), Argentina: MPA: 15 ♀ ♀ ad., 10 ♀ ♀ juv., 6 ♀ ♀ e., ♂ (ZMO, F 18438); MPA: 27 ♀ ♀ ad., 2 ♀ ♀ juv., 3 ♀ ♀ e. (BMNH, 1901. 12. 12. 251–261).

MATERIAL EXAMINED (Fig. 43). Lectotype, paralectotypes.

DIAGNOSIS. Measurements. ♀ ♀ ad.: 1.0–2.0mm, ♀ ♀ e. 1.0–1.5mm, ♂ ♂: 0.7–1.0mm.

Female (Fig. 44). Dorso-posterior valve prominence small, separated from the rest part of valves by shallow embayments. Its length less than the diameter of circle inscribed in its contour. Denticles cover less than 1/2 of posterior and less than 1/3 of dorsal margin. No denticles on ventral margin. Ocellus short. Frons with denticles. Morphology of trunk limbs unstudied, because it was impossible to dissect the type material.

DISTRIBUTION. (Fig. 43) Argentina, Brasil (São Paulo).

REMARKS. Daday (1905) believes *S. semiserratus* and *S. capensis* to be one species. Kanduru (1981) and Michael & Sharma (1988) sink *S. semiserratus* into the synonymy of *S. serrulatus*. Sars (1901) writes: ‘I am enabled to state with full certainty its [*S. semiserratus*] distinctness from the European species [*S. serrulatus*]. In addition to its somewhat larger size, it is easily distinguished by the far less prominent posterior projection of the carapace, and somewhat different shape of the head. The marginal denticles, moreover, which in *S. serrulatus* extend throughout the whole length of the hind margin,

are in this species always limited to their uppermost part only’. It is my belief that *S. semiserratus* is a separate species. First, statistical analysis shows that it is separated from *S. serrulatus* in two pairs of independent metric characters (Orlova-Bienkowskaja, 1995a). Second, it differs from it in the marginal denticles of the valves. Third, it occurs in South America sympatrically with *S. serrulatus* and cannot be a geographical subspecies of this species.

S. mirabilis sp.nov.

Figs 45; 46

ETYMOLOGY. The name ‘*Mirabilis*’ means ‘*Surprising*’.

TYPE MATERIAL. Holotype: U.S.A., Alabama, Mobil Co., lower part of Langan Park lake, 24. 5. 1987, leg. Fitzpatrick: MPA: ♀ ad. (BMNH 1997. 1709). Paratypes: collected with holotype: MPA: 11 ♀ ♀ ad., 9 ♀ ♀ juv. (BMNH 1997. 1710–1719); U.S.A., Oklahoma, Tulsa, Oxley Nature Center, Mallard lake, 36°10'N, 98°W, 12. 6. 1991, leg. Berner: MPA: 10 ♀ ♀ ad., 2 ♀ ♀ juv. (AC); Argentina, Rio Parana, Catay pond, leg. Frutos: MPA: 4 ♀ ♀ ad., 7 ♀ ♀ juv. (AC).

MATERIAL EXAMINED. (Fig. 43) Holotype, paratypes.

DIAGNOSIS. Measurements. ♀ ♀ ad. 1.0–1.2mm. Female (Figs 45; 46). Dorso-posterior valve prominence moderate, separated from the rest part of valves by moderate embayments. Its length less than the diameter of circle inscribed in its contour. Denticles cover less than 1/2 of posterior and less than 1/3 of dorsal

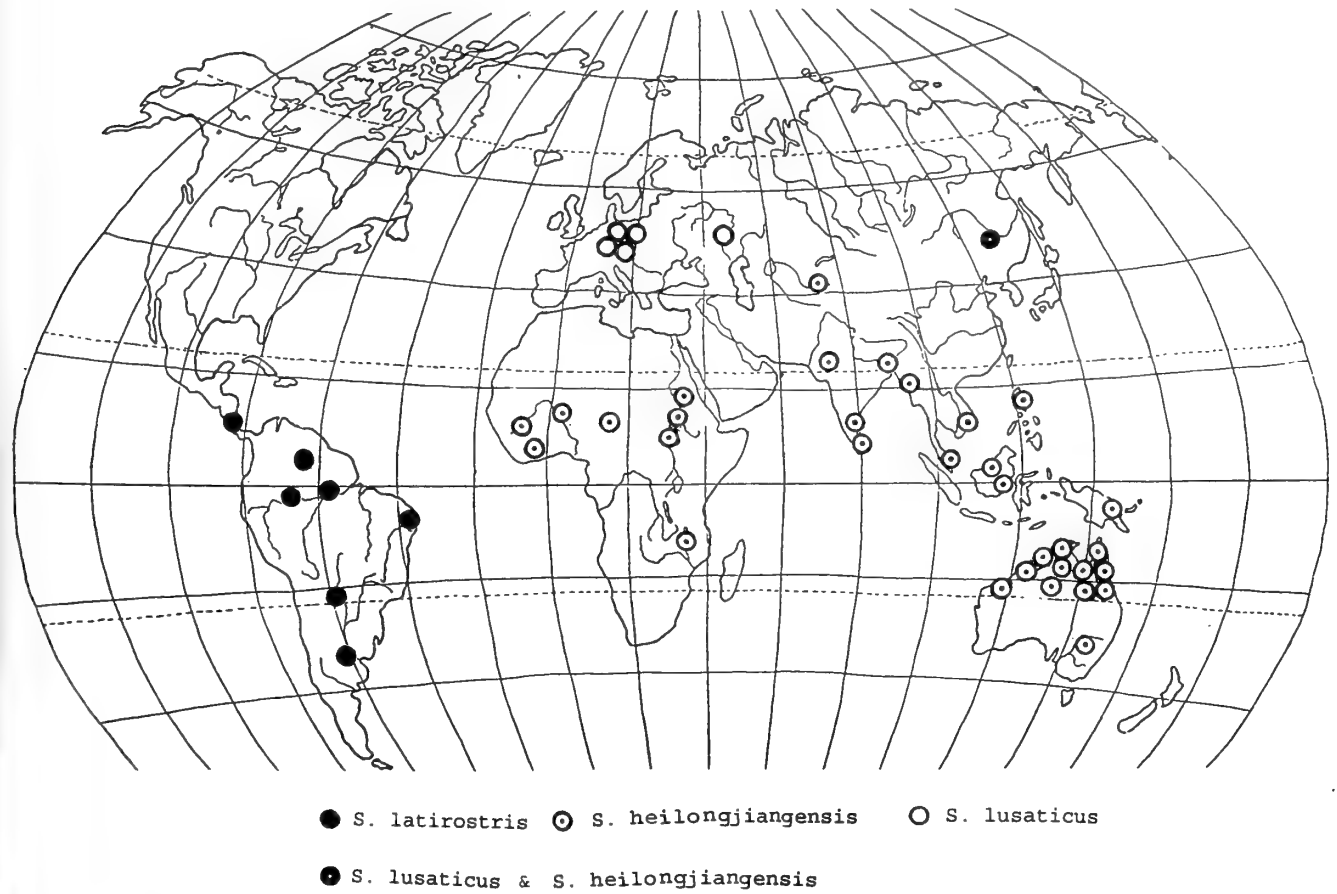


Fig. 51 Locations where the species of *S. (Aquipiculus)* were collected for this study or reported in literature.

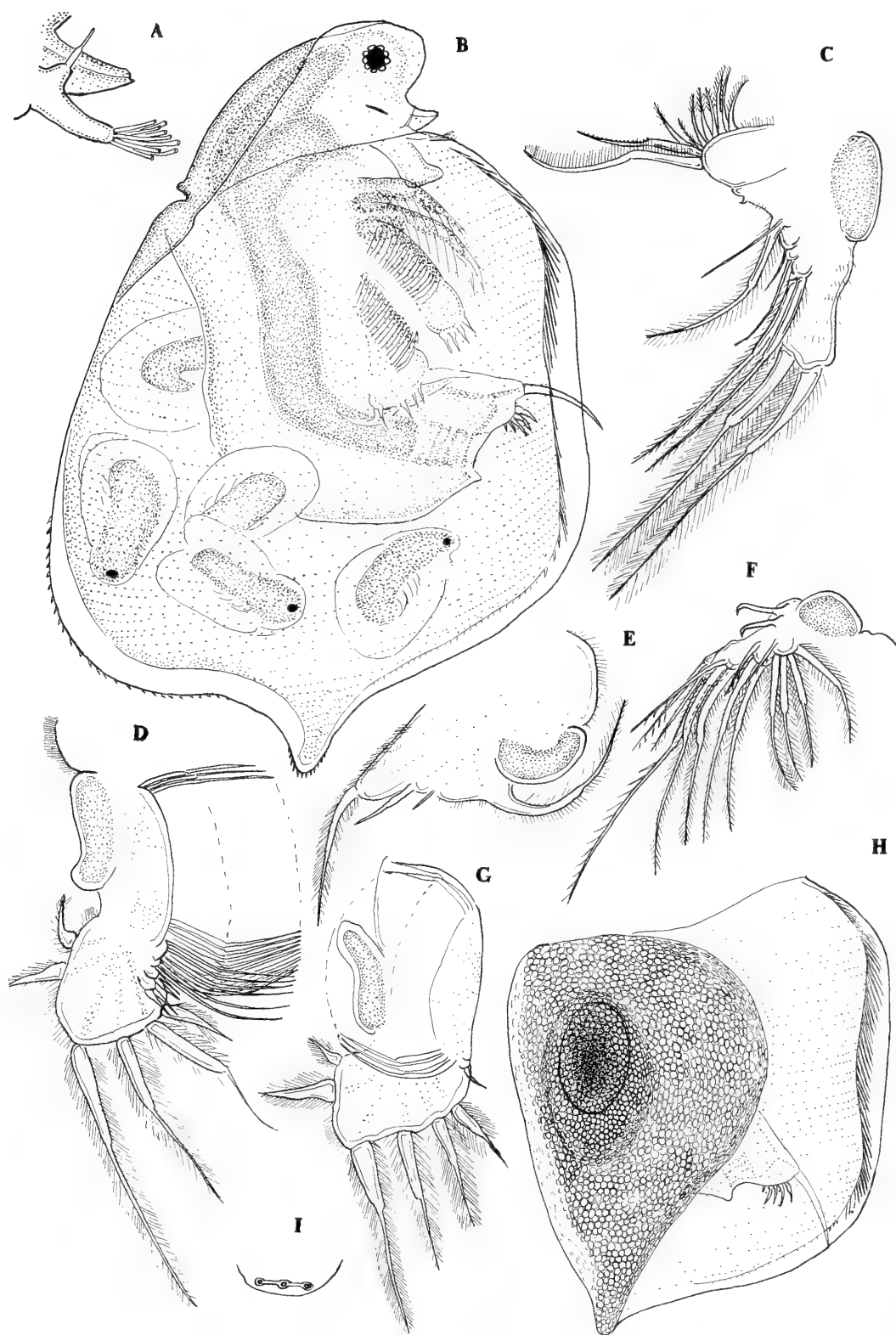


Fig. 52 *S. heilongjiangensis*, female. A, rostrum and antennule. B, parthenogenetic female. C, 2nd trunk limb. D, 3rd trunk limb. E, 5th trunk limb. F, 1st trunk limb. G, 4th trunk limb. H, ephippial female (head omitted). I, head pores.

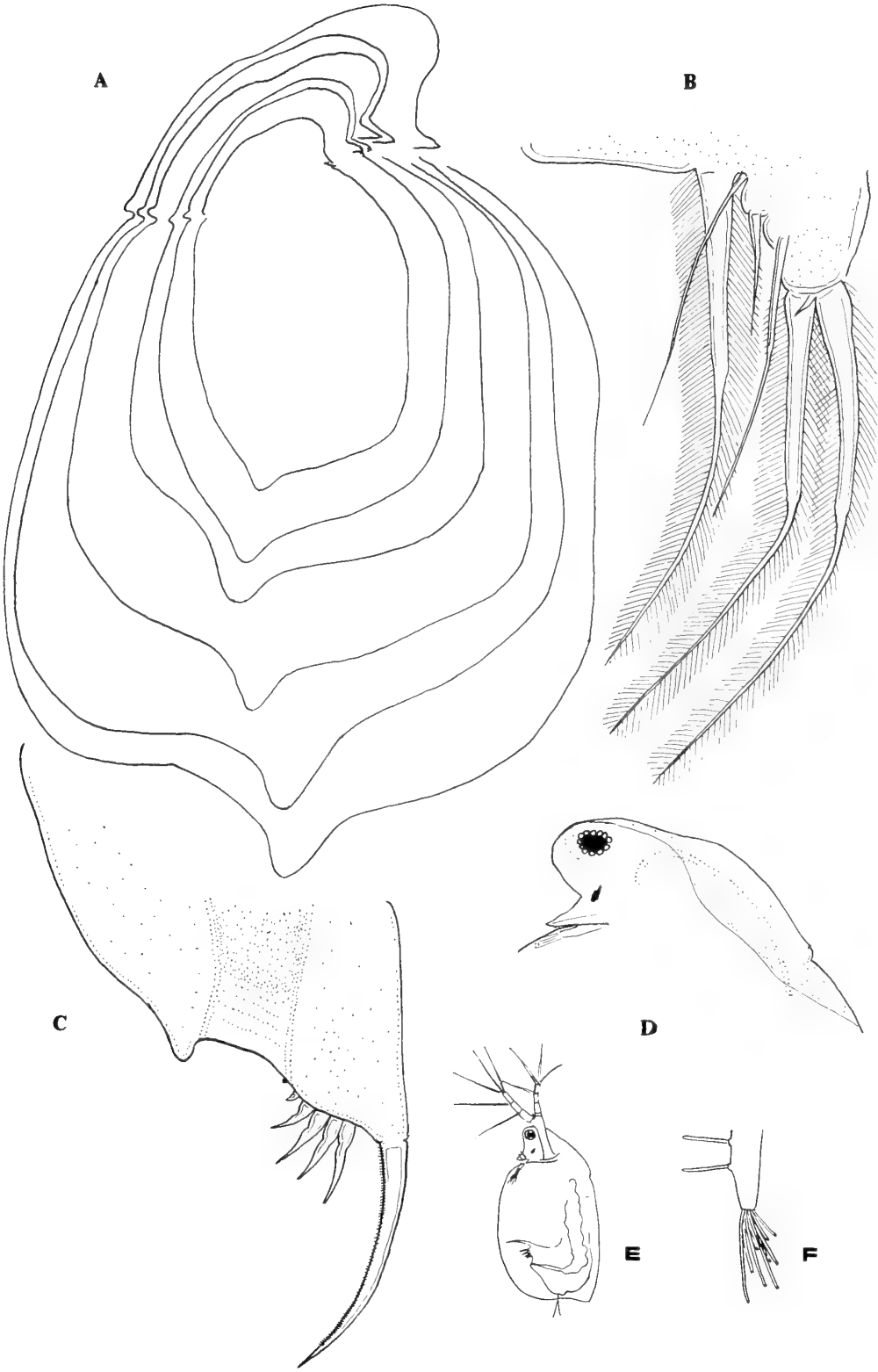


Fig. 53 *S. heilongjiangensis*. A, female, age variability, B, female, endite of 2nd trunk limb, C, female, postabdomen, D, female, head, E, male, lateral view, F, male, antennule (E, F – after Shi & Shi, 1994).

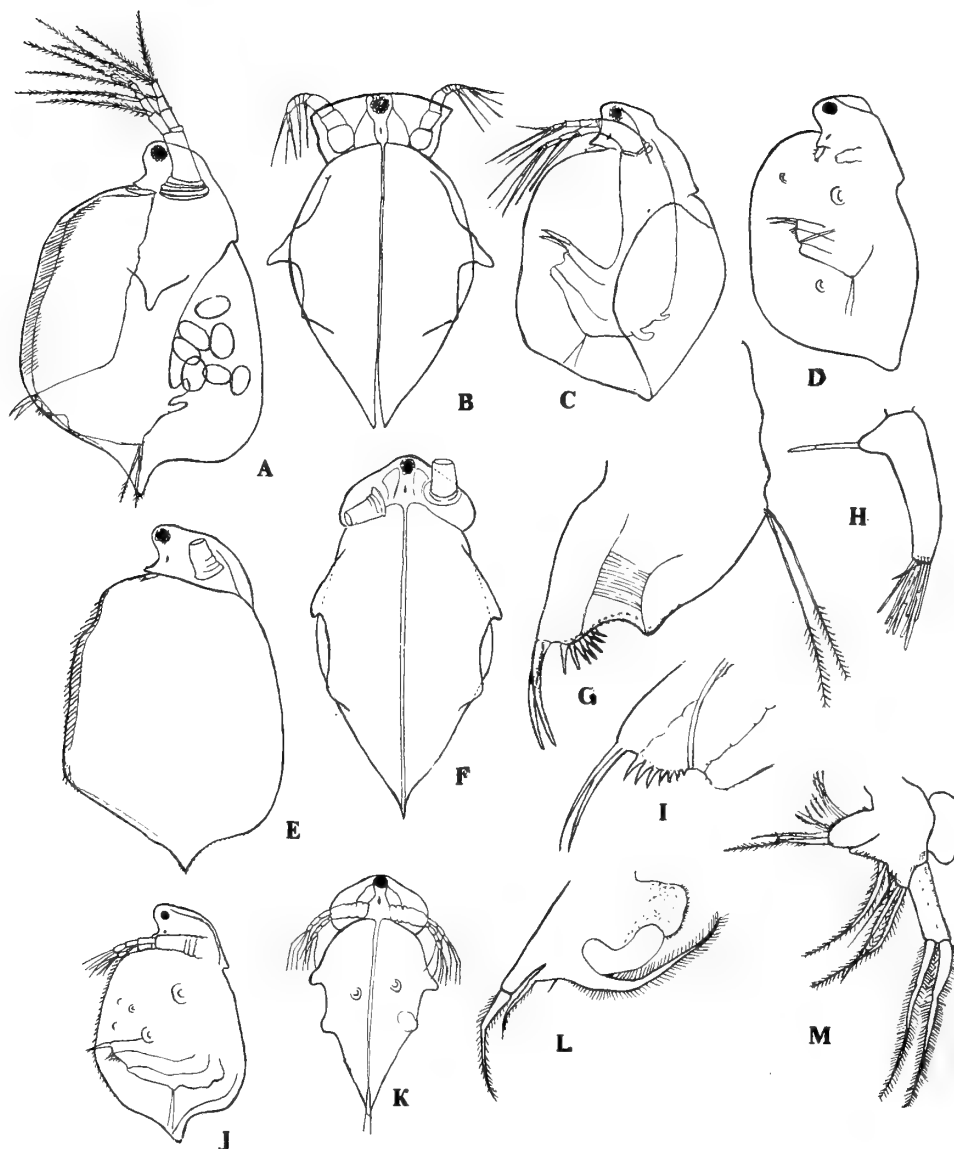


Fig. 54 *S. lusaticus*. A, parthenogenetic female, B, parthenogenetic female ventral, C, ephippial female, D, male, E, parthenogenetic female, F, parthenogenetic female, G, postabdomen, female, H, antennule, female, I, distal part of postabdomen, male, J, parthenogenetic female, K, parthenogenetic female, ventral, L, 5th trunk limb, female, M, 2nd trunk limb, female. A–C, G, H, L, M after Behning, 1925, D, I, J, K after Herr, 1917, E, F after Šrámek-Hušek *et al.*, 1962. edge. No denticles on ventral edge. Ocellus elongate. Frons without denticles. Setae of 2nd and 3rd endite prominence of 2nd trunk limbs as long as 0.6 and 0.4 of basal segment of plumose seta of 1st prominence respectively.

DISTRIBUTION. (Fig. 43) North and South America.

REMARKS. *S. mirabilis* differs from *S. serrulatus* and *S. semiserratus* in the elongate ocellus and the absence of denticles on the frons. However, I assign it to the subgenus *S. (Coronocephalus)*, because of the following characters: frons right-angled; antennule short, with transversal ridges covered with denticles on inner side; postabdominal claw with spines on proximal part of outer side and on inner side.

Subgenus *S. (Aquipiculus)* Orlova-Bienkowskaja, 1995

TYPE SPECIES. *Simocephalus latirostris* Stingelin, 1906

DIAGNOSIS. Both sexes (Figs 47–50). Frons rounded, without denticles. Head shield depressed or flattened in middle. Head pores

present. Insertion of antennules at base of rostrum. Antennule long in correspondence with long rostrum, with neither ridges nor denticles on inner side. Aesthetes shorter than base of antennule. Postabdominal claws without pecten of spines. Inner and outer side of claw with fine setules. Anal bay of postabdomen straightened in the middle, its proximal part without anal teeth.

Female. Dorso-posterior valve angle with large prominence. Valves with dorsal keel. Posterior corner of ephippium with protuberance. Ocellus short or slightly elongate, but always shorter than in *S. vetulus*. Setae of 2nd and 3rd endite prominence of 2nd trunk limb as long as 0.6–0.7 and 1.4–1.6 of basal segment of plumose seta of 1st prominence respectively. Postabdomen with 5–10 anal teeth on each side. Supra-anal angle pointed.

Male. Supra-anal angle pointed. Vas deferens opening in middle of anal bay or at base of supra-anal angle. Postabdomen with 5–7 anal

teeth on each side. Dorso-posterior valve angle with more or less pointed prominence.

ETYMOLOGY. The subgenus is named *Aquipiculus* or 'small water woodpecker' because all its representatives have a long rostrum resembling a beak.

S. latirostris Stingelin, 1906

Figs 47–50

S. latirostris Stingelin, 1906: 187; Brandorff *et al.*, 1982: 92; Orlova-Bienkowskaja, 1995b: 46.

TYPE MATERIAL. Lectotype (designated by Orlova-Bienkowskaja (1995b)): Paraguay, Riacho Negro, 3. 1894., leg. Ternetz, CBS in poor condition: ♀ ad., (MNO, III/24). Paralectotype: ♀ juv., mentioned in the original description, has probably been lost.

MATERIAL EXAMINED. (Fig. 51) Lectotype and other specimens: Argentina, Santa Fe, 23. 5. 1981: 21 ♀ ad., more than 50 ♀ juv., 31 ♀ e., 8 ♂♂ (BMNH and AC). Brasil, Rio Negro, Anavilanas Margen, 14. 9. 1979: ♀ ad.

DIAGNOSIS. Measurements. ♀ ♀ ad.: 1.0–1.8 mm, ♂♂: 0.6–0.9 mm. Both sexes (Figs 47–50). Rostrum very long, rostrum length 6.4–9.1% of body length in ♀ ♀ ad., 5.4–7.7% in ♂♂. Lateral margins of rostrum elevated above central part. Antennule long, in correspondence with long rostrum; about as long as rostrum. Head shield deeply depressed in middle.

Female. Height 65–74% of length. Ephippium length 47–67% of body length. Aesthetes shorter than antennule. Dorso-posterior valve prominence in ♀ ad. pointed. Denticles of valves very small, located only on dorso-posterior prominence. No lateral prominences of valves. Postabdomen with 5–9 (usually 7) anal teeth on each side. Anal teeth gradually decreasing in size proximally, 5th tooth more than half length of 4th.

Male. Vas deferens opening at base of supra-anal angle.

DISTRIBUTION. (Fig. 51) The tropics and subtropics of South and Central America. Numerous records of *S. latirostris* from Australia, Malay Archipelago, South-East Asia and Africa are available. Johnson (1963) supposes this species to be pantropical. However, according to the descriptions and figures, the authors misuse the name *S. latirostris* for *S. heilongjiangensis*.

REMARKS. *S. latirostris* was originally described at the beginning of the 20th century (Stingelin, 1906) and was poorly known up to now (Orlova-Bienkowskaja, 1995b). It was confused with next species by several authors (see below).

Dumont (1983) supposes *S. iheringi*, described from Brasil, to be a synonym of *S. latirostris*. The general body shape is rather similar in these two species, and the valves of females are produced into a sharp prominence in both species. But according to our data, *S. iheringi* is the junior synonym of *S. daphnoides* and clearly differs from *S. latirostris* in the pecten of the spines on the postabdominal claw.

S. heilongjiangensis Shi, Shi, 1994

Figs 52–53

Simocephalus latirostris: Fryer, 1957: 225; Johnson, 1963: 160; Biswas, 1971: 115; Dumont & Van De Velde, 1977a: 81; Mamaril & Fernando, 1978: 134; Kanduru, 1981: 65; Rajapaksa, 1981: 98; Hossain, 1982: 112; Dumont, 1983: 103; Michael & Sharma, 1988: 80; *S. heilongjiangensis* Shi, Shi, 1994: 403; *S. mesorostris* Orlova-Bienkowskaja, 1995b: 51.

TYPE MATERIAL. Holotype. Moershan Town (45°15'N, 127°30'E), Shangzhi County, Heilongjiang Province, 6.8.1990., leg. Shi Xinlu. ♀ ad. Allotype ♂ and paratypes 30 ♀ ♀ and 10 ♂♂ collected with holotype (deposited in the Laboratory of Hydrobiology, Harbin Normal University, China).

MATERIAL EXAMINED. Type material of junior synonym *S. mesorostris*: Holotype. The Philippines, Luzon, Bulacan near Chemical Plant, pond, 1.1976: CBS: ♀ ad. (BMNH, 1995.753). Paratypes: 110 specimens (♀ ♀ ad., ♀ ♀ juv. and ♀ ♀ e.) from The Philippines, Indonesia, Malaysia, New Guinea, Australia, Viet-Nam, Sri Lanka and India (BMNH, AC). More precise geographical data are published elsewhere (Orlova-Bienkowskaja, 1995b). Other specimens: 139 specimens (♀ ♀ ad. and ♀ ♀ juv.) from Sudan (AC).

DIAGNOSIS. Measurements. ♀ ♀ ad.: 1.2–1.9 mm.

Female. (Figs 52; 53). Height 59–75% of length. Rostrum shorter than in *S. latirostris*; length 3.3–5.7% of body length. Lateral margins of rostrum below central part. Antennule shorter than in *S. latirostris*, in correspondence with moderate size of rostrum, its length about as long as rostrum. Aesthetes longer than antennule. Depression of head shield shallow. Dorso-posterior valve prominence in ♀ rounded. Denticles of valves of moderate size, located both on dorso-posterior prominence and on dorsal valve margin. No lateral prominences of valves. Postabdomen with 5–8 (usually 6) anal teeth on each side. Four distal teeth large, the rest extremely small, 5th tooth less than half as long as 4th.

Male. Vas deferens opening at base of supra-anal angle.

DISTRIBUTION. The tropics of Australia, Malay Archipelago, Asia and Africa (Fig. 51).

REMARKS. The specimens from Africa differ from others in shorter rostrum. However I believe that the African *S. heilongjiangensis* does not belong to another subspecies because there is a considerable overlapping in this character (more than 25%) and there are no other differences.

S. heilongjiangensis was confused with the closely related *S. latirostris* by many authors (Fryer, 1957; Dumont & Van De Velde, 1977a; Rajapaksa, 1981; Kanduru, 1981; Hossain, 1982; Dumont, 1983; Michael & Sharma, 1988). I discovered that it is a separate species (Orlova-Bienkowskaja, 1995b) and described it as *S. mesorostris*. Shi & Shi (1994) came to the same conclusion independently and named this species *S. heilongjiangensis*. This name has the priority.

S. lusaticus Herr, 1917

Fig. 54

Simocephalus lusaticus: Herr, 1917: 58; Behning, 1923: 5; 1925: 526; Štárek-Hušek *et al.*, 1962: 259; Flössner, 1972: 182; Kamiński, 1975: 89.

TYPE MATERIAL. Syntypes: East Europe, Silesia, ponds near Werda, 27. 7. 1913 (12 specimens), 5. 9. 1913 (3 specimens), 'false ponds', 10. 8. 1913 (6 specimens). I do not know in what museum these syntypes were deposited, or whether they still exist.

MATERIAL EXAMINED. None.

DISTRIBUTION. (Fig. 51) East Europe: Silesia, Czech Republic, Slovakia, Poland, Russia: Wolga basin. Chihai: Heilong Province. Manujlova (1964) reports this species from the Caucasus. Obviously, this is a misunderstanding, because she refers to a book (Behning, 1941) which contains no such information.

DIAGNOSIS. Measurements. ♀ ♀ ad.: 1.5–3 mm, ♂♂ about 1 mm.

Both sexes (Fig. 54). Rostrum shorter than in *S. latirostris*; its lateral margins below central part. Antennule shorter than in *S. latirostris*, about as long as or a little longer than rostrum. Depression of head shield shallow.

Female. Aesthetes about as long as antennule. Dorso-posterior valve prominence rounded or pointed. Denticles of valves very small, located only on dorso-posterior prominence. 2–8 pairs of lateral prominences on valves. Postabdomen with 7–10 anal teeth on each side. Anal teeth gradually decreasing in size proximally.

Male. Vas deferens opening in middle of anal bay.

REMARKS. Judging from the available descriptions (Herr, 1917; Behning, 1925; Šrámek-Hušek *et al.*, 1962; Flössner, 1972; Kamiński, 1975), *S. lusaticus* has all the diagnostic characters of the subgenus *Aquipiculus*. It differs from all other species of the genus in having lateral prominences on the valves.

NOMINA DUBIA AND SPECIES TRANSFERRED TO THE GENUS *DAPHNIA*

S. aegyptiacus (Fischer, 1860) has been described from the vicinity of Alexandria (Egypt). There is no information about the type material. The original description (Fischer, 1860) is rather detailed and allows us to attribute this species to *Simocephalus* s. str. I think that contrary to the opinion of Richard (1894) and Šrámek-Hušek *et al.* (1962), it is not a synonym of *S. vetulus* because it has a large dorso-posterior valve prominence. Behning (1941) supposes this species to be a synonym of *S. elizabethae*, but I believe that the latter differs from all species including *S. aegyptiacus* in the shape of the ventral head margin. Unfortunately, it is impossible to conclude whether *S. aegyptiacus* is a separate species or a synonym of *S. mixtus* or *S. vetuloides*.

S. cacticus Moniez, 1889 has been described from Lake Titicaca. There is no information about the type material. To judge from the original description (Moniez, 1889), this species belongs to *Simocephalus* s. str. But it is difficult to say whether it is in fact a separate species.

S. vetulus spinosulus Stingelin, 1904 has been described from the Hawaiian Islands. Stingelin (1904) points out that this variety differs from the typical form because 'es zeigt sich die Tendenz zur Bildung einer schwachen Shalenprominenz'. No illustration is given. The type material has been lost (Frenzel, 1987). Some authors regard *S. vetulus* var. *spinosulus* as a synonym of *S. vetulus* (Flössner, 1972; Frenzel, 1987). The original description shows that this variety belongs to *Simocephalus* s. str., but it does not contain any characters important for the identification of species within this subgenus. Material from the Hawaiian Islands is necessary to decide this question.

S. serrulatus var. *nudifrons* Delachaux, 1918 has been described from the Andes (Peru). The type was probably not indicated. The original description (Delachaux, 1918) is without an illustration and contains only one character: the absence of denticles at the head in all specimens. That means that it is not *S. serrulatus* because the denticles are the main character of this species. But this information is not enough to permit identification.

S. postidelivis Lai & Li, 1987 was described on the base of fossil ephippia from the Tertiary of China (Lai & Li, 1987). Referring to the photographs, these ephippia do not differ from ephippia of recent species. It is impossible to identify either the species or even the subgenus.

Two species assigned to the genus *Simocephalus* belong, in fact, to the genus *Daphnia*, as is evident from their original descriptions

(Studer, 1878; Brady, 1918). This is *S. gelidus* Brady, 1918 = *Daphnia gelida* comb. nov. and *S. intermedius* Studer, 1878 = *D. intermedia* comb. non.

KEY TO THE SUBGENERA AND SPECIES OF *SIMOCEPHALUS*

Figs 55–59 (picture numbers correspond with couplets in the key)

1. Fig. 55. ♀ & ♂: Postabdominal claw without spines. Inner and outer side of claw with fine setules (A). Frons rounded, without denticle (B) 2
 - Fig. 55. ♀ & ♂: Postabdominal claw with basal pecten of spines at outer side. Inner side and distal part of outer side with fine setules (C). Frons rounded (D) or pointed (E), without denticles *S. (Echinocaudus) subgen. nov.* 10
 - Fig. 55. ♀ & ♂: Postabdominal claw with spines on inner side and in proximal part of outer side. Basal part of outer side with fine setules (F). Frons right-angled, with denticles, or very rarely without denticles (G) (American species *S. mirabilis*) *S. (Coronocephalus)* Orlova-Bienkowskaja, 1995 16
2. Fig. 55. ♀: Ocellus elongate (H) (exception: North American species *S. punctatus*). Anal bay with small anal teeth (I). Dorso-posterior valve angle without prominence (J) or with comparatively small prominence (K). ♂: Vas deferens opening on top of supra-anal angle (L). *Simocephalus* s. str. 3
 - Fig. 55. ♀: Ocellus short (M). Anal bay without anal teeth (N). Dorso-posterior valve angle with large prominence (O). ♂: Vas deferens opening in middle of anal bay or at base of supra-anal angle (P) (*S. (Aquipiculus)* Orlova-Bienkowskaja, 1995 8
3. Fig. 56. ♀: Ocellus point-like (B). Dorso-posterior valve angle rounded, without prominence (A). Occurs in North America *S. punctatus* sp. nov.
 - Fig. 56. ♀: Ocellus elongate (C). Dorso-posterior valve angle of different shape 4
4. Fig. 56. ♀: Dorso-posterior valve angle with very small prominence (D). The most common European species. Occurs also in North Africa *S. vetulus* (O.F. Müller, 1776)
 - Fig. 56. ♀: Dorso-posterior valve angle with larger prominence (E) 5
5. Fig. 56. ♀: Depression of ventral head margin near rostrum deep (F) 6
 - Fig. 56. ♀: Depression of ventral head margin near rostrum shallow, sometimes absent (G). Species occur in Australia, Tasmania and New Guinea 7
6. Fig. 56. ♀: Diameter of dorso-posterior valve prominence exceeds its length (H). Dorsal valve margin protruding backward (I) *S. mixtus* Sars, 1903
 - Fig. 56. ♀: Diameter of dorso-posterior valve prominence less than its length (J). Dorsal valve margin not protruding backward (K). Occurs in Eastern Siberia *S. vetuloides* Sars, 1898
7. Fig. 56. ♀: Dorsal valve margin protruding backward strongly (L) *S. gibbosus* Sars, 1896
 - Fig. 56. ♀: Dorsal valve margin not protruding backward (M) *S. elizabethae* (King, 1853)
8. Fig. 57. ♀ & ♂: lateral prominences on valves present (A). Rare species. Occurs in East Europe and China. *S. lusaticus* Herr, 1917

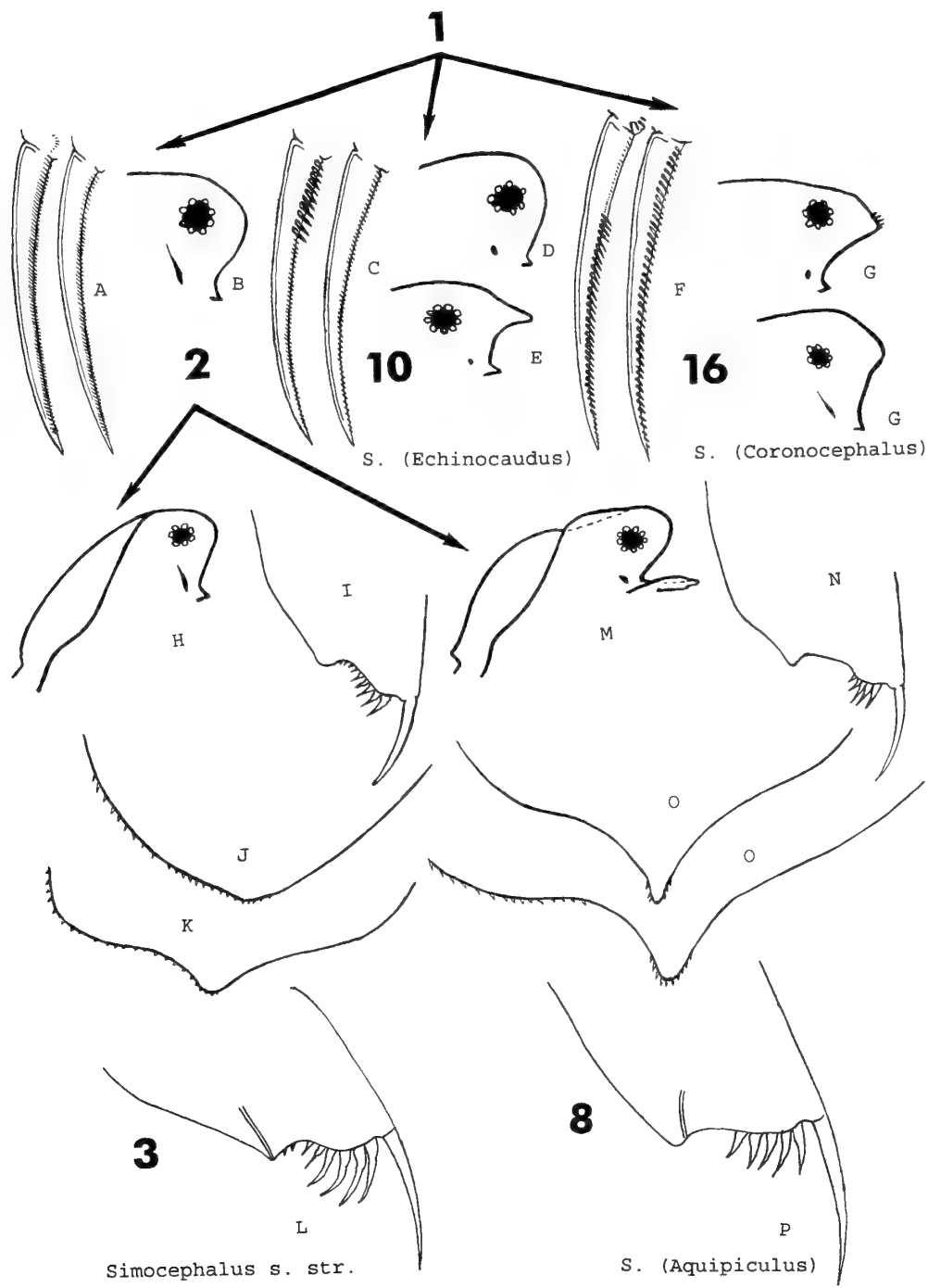


Fig. 55 Key to subgenera. Numbers correspond with couplets in the key.

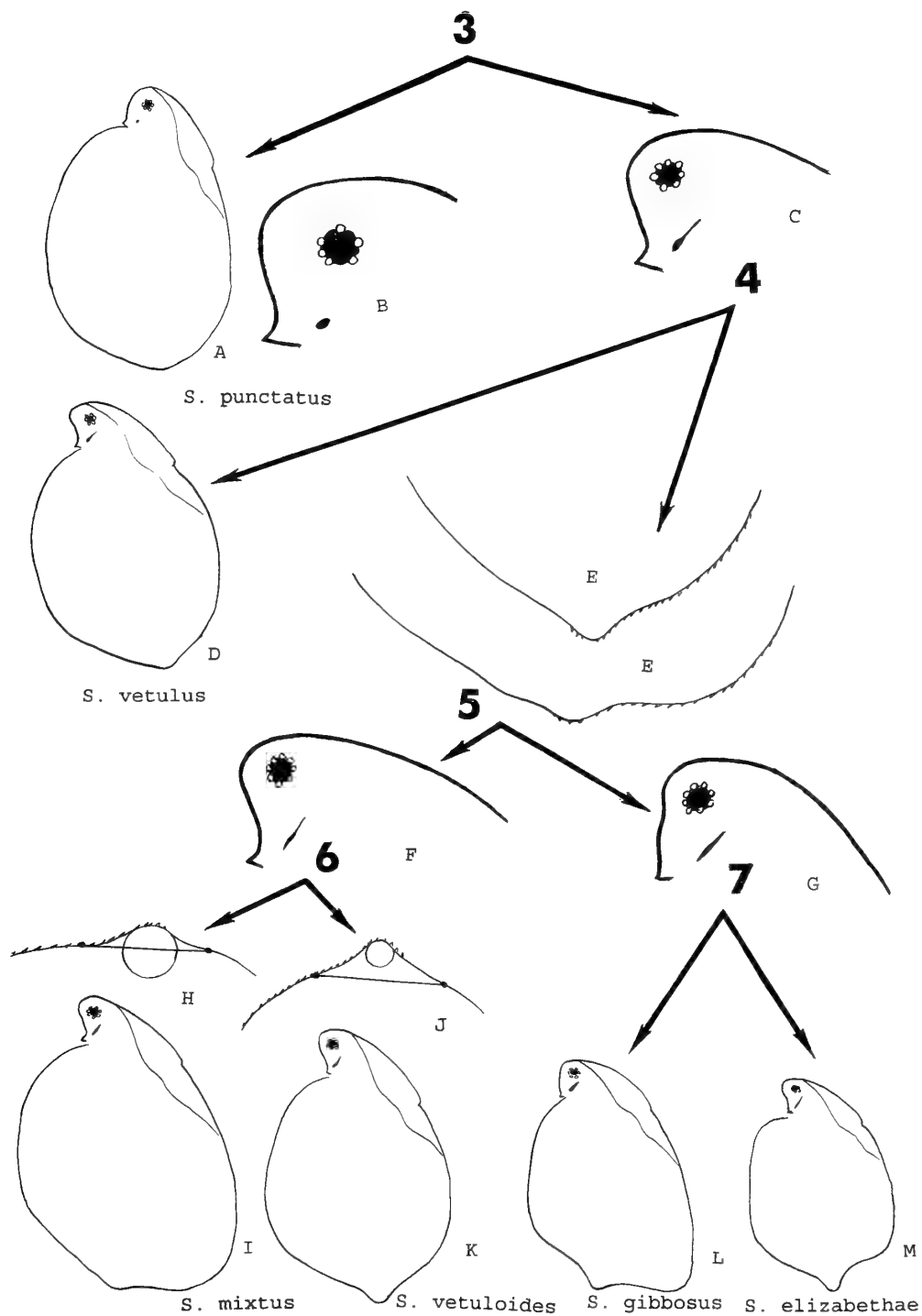


Fig. 56 Key to *Simocephalus* s. str. Numbers correspond with couplets in the key.

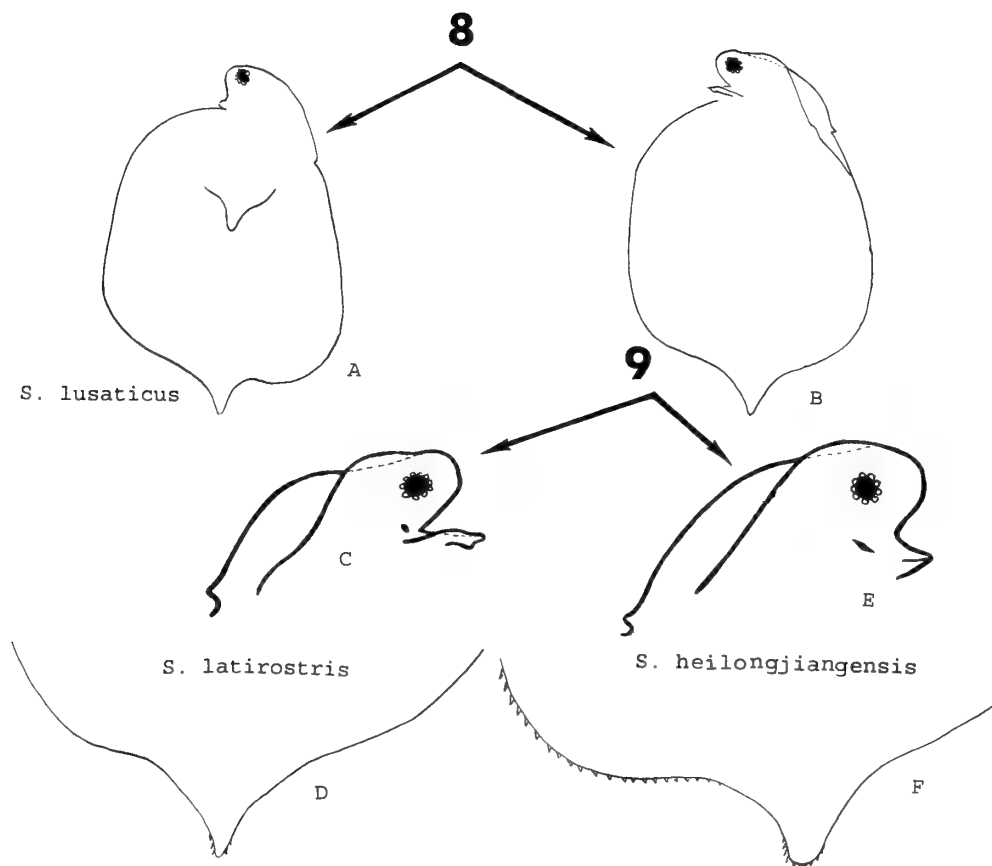


Fig. 57 Key to *S. (Aquipiculus)*. Numbers correspond with couplets in the key.

- Fig. 57. ♀ & ♂: No lateral prominences on valves (B) 9
- 9. Fig. 57. ♀: Rostrum very long, its lateral margin elevated above central part (C). Dorso-posterior valve prominence pointed (D). Occurs in South America *S. latirostris* Stingelin, 1906
- Fig. 57. ♀: Rostrum of moderate size, its lateral margin below central part (E). Dorso-posterior valve prominence rounded (F). Occurs in Australia, Malay Archipelago, Asia and Africa. *S. heilongjiangensis* Shi, Shi, 1994
- 10. Fig. 58. ♀: Frons rounded (A). One supra-anal angle (B) 11
- Fig. 58. ♀: Frons pointed (C). Two supra-anal angles (D) *S. acutirostratus* species group 14
- 11. Fig. 58. ♀: Ventral head margin very convex (E). Spines of basal pecten of postabdominal claw well-spaced (F). Occurs in New-Zealand *S. obtusatus* (Thomson, 1878)
- Fig. 58. ♀: Ventral head margin almost straight (G). Spines of basal pecten of postabdominal claw close-set (H) 12
- 12. Fig. 58. ♀: Dorso-posterior valve angle with large pointed prominence (I). Occurs in America *S. daphnoides* Herrick, 1883
- Fig. 58. ♀: Dorso-posterior valve angle with rounded prominence or without prominence (J) 13
- 13. Fig. 58. ♀: Basal pecten of postabdominal claw of 8–12 spines of moderate size (K) *S. exspinosus* (De Geer, 1778)
- Fig. 58. ♀: Basal pecten of postabdominal claw of 20–25 small spines (L). Occur in Europe and Asia *S. congener* (Koch, 1841)
- 14. Fig. 58. ♀: Dorso-posterior valve angle smooth, rounded, without prominence (M). Occurs in Australia *S. victoriensis* Dumont, 1983
- Fig. 58. ♀: Dorso-posterior valve angle with distinct prominence covered with denticles (N) 15
- 15. Fig. 58. ♀: Dorso-posterior valve prominence separated above and below by deep, wide depressions. Diameter of circle inscribed in it moderate (O). Occurs in Africa *S. brehmi* Gauthier, 1939
- Fig. 58. ♀: Dorso-posterior valve prominence separated above and below by shallow, wide depressions. Diameter of circle inscribed in it large (P). Occurs in Australia and Asia *S. acutirostratus* (King, 1853)
- Fig. 58. ♀: Dorso-posterior valve prominence separated above and below by deep, narrow depressions. Diameter of circle inscribed in it small (Q). Occurs in North America *S. rostratus* Herrick, 1884
- 16. Fig. 59. ♀: Ocellus elongate. Frons without denticles (A). Occurs in America *S. mirabilis* sp. nov.
- Fig. 59. ♀: Ocellus short. Frons with denticles (B) 17
- 17. Fig. 59. ♀: Dorso-posterior valve prominence large, separated from rest of valves by deep embayments (C). Its length exceeds diameter of circle inscribed in its contour (D). Denticles cover ventral, posterior and more than 1/3 of dorsal margin. *S. serrulatus* (Koch, 1841)
- Fig. 59. ♀: Dorso-posterior valve prominence small, separated from rest of valves by shallow embayments (E). Its length less than diameter of circle inscribed in its contour (F). No denticles on ventral margin. Denticles cover less than 1/2 of posterior and less than 1/3 of dorsal margin. Occurs in South America *S. semiserratus* Sars, 1901

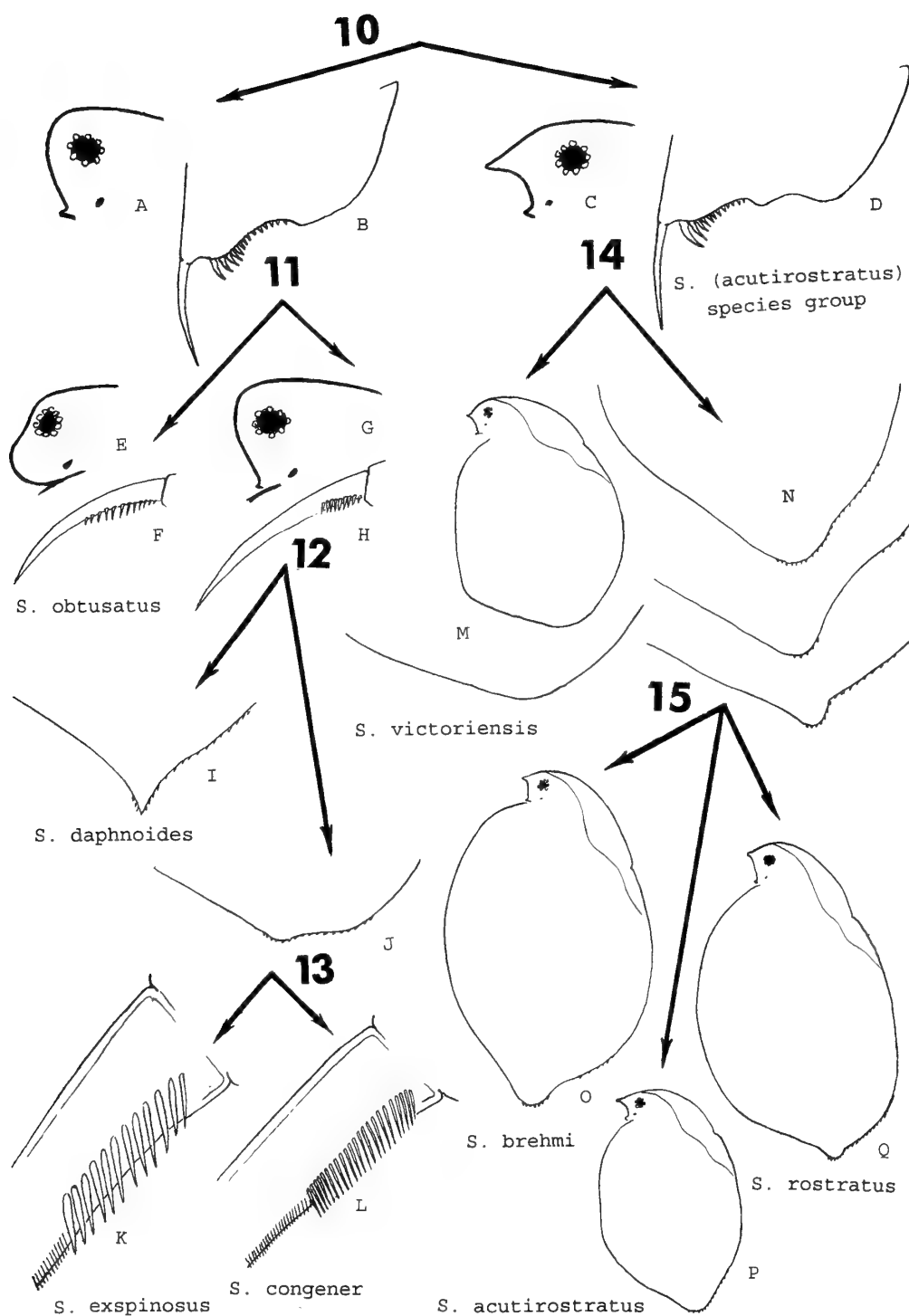


Fig. 58 Key to *S. (Echinocaudus)*. Numbers correspond with couplets in the key.

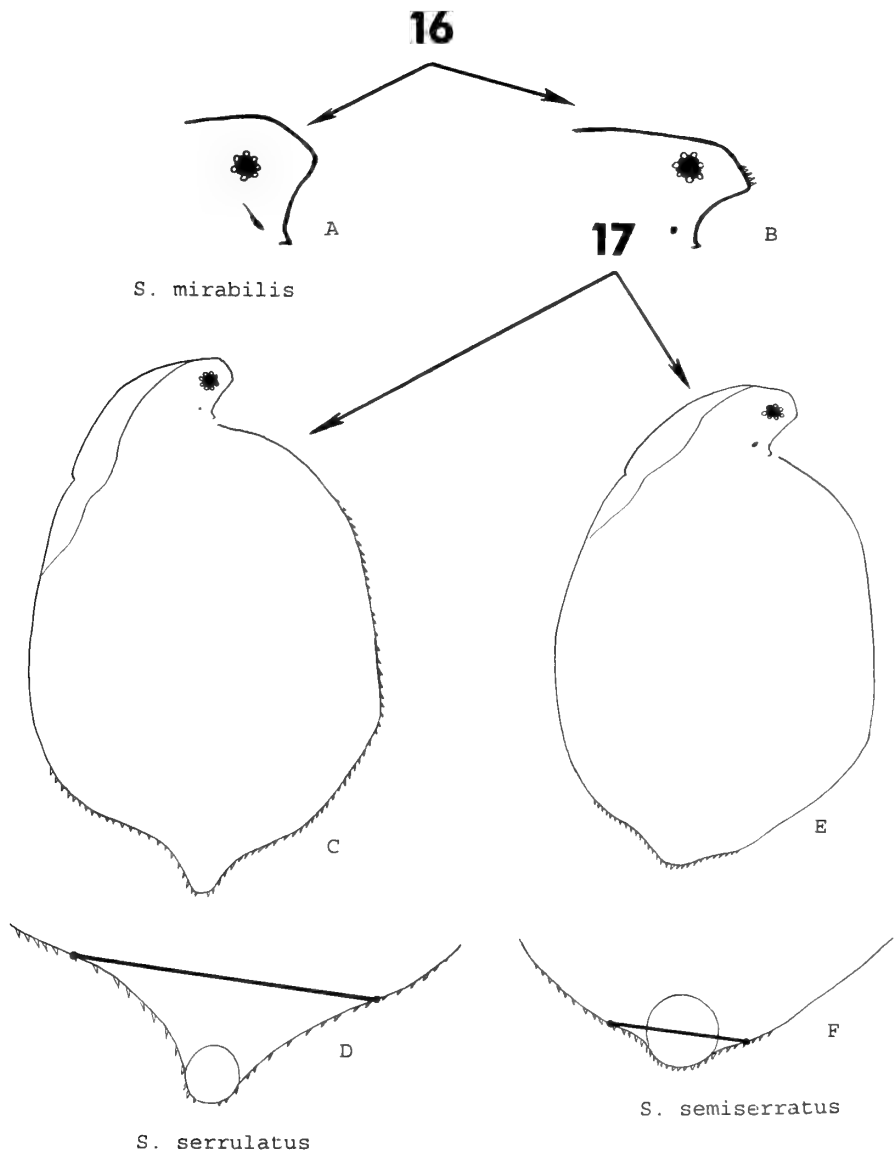


Fig. 59 Key to *S. (Coronocephalus)*. Numbers correspond with couplets in the key.

CHECK LIST OF SIMOCEPHALUS

Subgenus *Simocephalus* s. str.

1. *S. vetulus* (O.F. Müller, 1776) (*Daphne vetula*)
Daphnia sima O.F. Müller, 1785
Monoculus nasutus Jurine, 1820
S. vetulus var. *angustifrons* Lilljeborg, 1900
S. vetulus var. *brandti* Cosmovici, 1900 syn. nov.
S. vetulus gebhardti Ponyi, 1955
S. mixtus hungaricus Ponyi, 1956
2. *S. elizabethae* (King, 1853) (*Daphnia Elizabethae*)
S. dulvertonensis Smith, 1909
3. *S. gibbosus* Sars, 1896
4. *S. vetuloides* Sars, 1898
5. *S. mixtus* Sars, 1903
S. corniger Methuen, 1910 syn. nov.
S. beianensis Shi, Sbi, 1994 syn. nov.
6. *S. punctatus* sp. nov.

Subgenus *S. (Echinocaudus)* subgen. nov.

7. *S. obtusatus* (Thomson, 1878) (*Daphnia obtusata*)
8. *S. daphnoides* Herrick, 1883
S. Iheringi Richard, 1897 syn. nov.
S. fonsecai Bergamin, 1939 syn. nov.
S. fonsecai var. *sinucristatus* Bergamin, 1939 syn. nov.

S. (exspinosus) species group

9. *S. exspinosus* (De Geer, 1778) (*Monoculus exspinosus*)
Daphnia australiensis Dana, 1852
S. sibiricus Sars, 1898 syn. nov.
S. productus Sars, 1903
S. himalayensis Chiang & Chen, 1974 syn. nov.
S. vamani Rane, 1985
10. *S. congener* (Koch, 1841) (*Daphnia congener*)

S. (acutirostratus) species group

11. *S. acutirostratus* (King, 1853) (*Daphnia Elizabethae* var. *acuti-rostrata*)
S. paradoxus Schödler, 1877
S. vidyae Rane, 1983
S. vidyae gajareae Rane, 1986
12. *S. victoriensis* Dumont, 1983
13. *S. brehmi* Gauthier, 1939 stat. nov. (*Simosa acutirostrata brehmi*)
S. acutifrons Johnson, 1954 syn. nov.
14. *S. rostratus* Herrick, 1884

Subgenus *S. (Coronocephalus)* Orlova-Bienkowskaja, 1995

15. *S. serrulatus* (Koch, 1841) (*Daphnia serrulata*)
D. brandtii Fischer, 1848
D. intermedia Lievin, 1848
S. americanus Birge, 1878
S. capensis Sars, 1895
S. inflatus Vávra, 1900
S. serrulatus var. *productifrons* Stingelin, 1904
S. serrulatus var. *montenegrinus* Werestchagin, 1912
S. serrulatus var. *mixta* Grochmalicki, 1915
S. serrulatus var. *rotundifrons* Brehm, 1933
S. kerhervei Bergamin, 1939
S. aqua-brankai Bergamin, 1939
S. serrulatus var. *armata* Brehm, 1956
S. serrulatus var. *pelagicus* Brehm, 1959
S. surekhae Rane, 1985

16. *S. semiserratus* Sars, 1901
17. *S. mirabilis* sp. nov.

Subgenus *S. (Aquipiculus)* Orlova-Bienkowskaja, 1995

18. *S. latirostris* Stingelin, 1906
19. *S. lusaticus* Herr, 1917
20. *S. heilongjiangensis* Shi, Shi, 1994
S. mesorostris Orlova-Bienkowskaja, 1995

Nomina dubia

- Daphnia aegyptiaca* Fischer, 1860
S. cacticus Moniez, 1889
S. vetulus spinosulus Stingelin, 1904
S. serrulatus var. *nudifrons* Delachaux, 1918
S. postidelivis Lai & Li, 1987

Species transferred to the genus *Daphnia*

- S. gelidus* Brady, 1918 = *Daphnia gelida* comb. nov.
S. intermedius Studer, 1878 = *D. intermedia* comb. nov.

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Structural niche, limb morphology and locomotion in lacertid lizards (Squamata, Lacertidae); a preliminary survey

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CONTENTS

Introduction	64
Phylogenetic relationships of the Lacertidae	65
Structural niches of lacertid lizards	65
Overview of lacertid structural niche space	65
Structural habitats occupied by groups within the Lacertidae	65
Primitive Palaearctic forms	65
Members of the Armatured clade	67
Evolutionary change in structural niche	69
Morphology	69
Body proportions and vertebral number	69
Relative tail length	70
Limb proportions and structural niche	71
Sexual dimorphism in limb length	72
Relative proportions of femur and tibia	73
Patterns of limb growth	73
Evolutionary plasticity of limb proportions	73
Functional aspects of differences in limb proportions	73
Differences in the caudifemoralis longus muscle	74
General anatomy of the hind leg	74
Structure of the pes	74
The pes in ground dwelling lacertids from open situations	75
The pes in lacertids regularly climbing steep, open surfaces	75
Variations in the direction of kinking in toe 5 of lacertids	77
Patterns of digital kinking in climbers of other families	77
Structure of the manus	78
The manus in ground dwelling lacertids from open situations	78
The manus in lacertids regularly climbing on steep open surfaces	78
Characteristics of the feet in other lacertids	78
Special structures of the digits	80
Expanded subdigital lamellae	80
Keeling on subdigital scales	80
Digital fringes	80
Locomotion and function	81
Locomotion in ground dwellers of the Armatured clade	81
Movements of the hind limb	83
Rotation of the femur and supposed restrictions on its movement	83
The supposed problem of crural rotation	83
A partial model of hind limb movement	83
Other hind limb gaits in ground dwelling lizards – continuous gearing	84
Movements of the foreleg in ground dwellers	84
Functional aspects of the limbs and feet of ground dwelling lacertids	84
Ground locomotion in climbing species	84
Locomotion in climbers on steep open surfaces	84
Movements of the hind limb	85
Movements of the fore limb	86
Other patterns of locomotion in specialised climbing lacertids	86
Problems of upward vertical locomotion	86
Functional aspects of the limbs and feet of specialised climbing lacertids	86
Climbing in specialised ground dwelling species	86
Concluding remarks	88
Acknowledgements	88
References	88

SYNOPSIS. Lacertid lizards occur in a wide range of structural habitats and 1) may be found on open ground ranging from rocky surfaces, gravel and soil to firm and loose sand, or 2) be associated with quite dense low ground vegetation, or 3) climb through and over vegetation matrixes such as tall grass and herbs, bushes and tree canopy, or 4) climb on more or less continuous steep or even overhanging surfaces such as rock faces and tree boles. Some forms are largely confined to one of these broad structural niches while others occur more widely, but the locomotory requirements of the habitat occupied are usually reflected in morphology. The body may show some elongation in taxa that regularly travel through complex interstices of vegetation and similar habitats while it is quite short in forms that live on open ground; the tail is often extremely long in matrix climbers and may help spread weight in these.

When forelimb span/hindlimb span is plotted against hindlimb span/ head + body length, lacertids group substantially according to their structural niche. In general, disparity in span of the limb pairs increases with hindlimb length: long hind and short fore limbs occur in open ground forms, shorter more equal limb pairs in climbers in matrixes and on continuous surfaces, and very short subequal limbs in forms associated with dense low ground vegetation. Sexual dimorphism in limb proportions is found in some taxa, females having shorter and usually more equal limbs, but it is not known if this reflects differences in structural habitat. Proportions of limbs may vary considerably among close relatives as do their growth patterns, indicating that they may be easily modified by natural selection. Variation also occurs in the relative lengths of the femur and crus.

On open ground, long hind limbs can be effectively deployed and provide a high-gear system that contributes most locomotor thrust and produces high speeds. In dense ground vegetation etc. the forelimbs are probably used more and the short legs can be deployed effectively in confined spaces. Among matrix climbers, the same advantages can apply and in climbers as a whole the relatively short hind limbs provide low-gear thrust against gravity while the forelimbs also contribute and, in addition, prevent the foreparts falling away from steep surfaces.

The caudifemoralis muscle, which is the main retractor of the thigh, has its origin in the proximal tail with multiple heads attached mainly to the non-autotomic pygal vertebrae. the number of these vertebrae increases in advanced ground-dwellers and this may enhance effective size of the muscle and hence limb power. In many lacertids, the most posterior part of the muscle, which is slender, extends a short distance on to the autotomic vertebrae and may consequently be lost during tail shedding.

The complex movements of the hind limbs in ground-running lacertids are described including their effects in ameliorating the supposed problem of crural rotation. In the hind feet of open ground dwellers, the metatarsals and toes 1–4 increase in length, allowing the long claws which act like athlete's spikes to gain purchase over a broad area. At the end of a stride, ground lizards may rise on to the tips of toes 2–4 of a single foot, something permitted by robust phalanges and restrictions on mesial flexion at the toe joints; toe 5 is scarcely used and often miniaturised. The gait of lacertids varies according to the degree the crus and foot are extended forwards, providing a variable gear system that alters as the lizard gains speed; however on very steep surfaces climbing species rarely extend the leg fully.

In climbers on open surfaces, metatarsal 3 is longest allowing toe 3 to be deployed anteriorly or posteriorly. Toes are often spread broadly and a positive grip obtained by a system of digital kinking that allows them to shorten after claw insertion. While kinking is beneficial to climbing lizards, its exact pattern may be partly arbitrary and varies considerably across taxa. Slender phalanges and robust tendons reflect the fact that toes of climbing lizards are often under tension. Upward thrust is maximised by maintaining the grip of the feet as long as possible. This is facilitated by a system that allows differential flexion of the digits and by substantial flexibility of their joints.

The morphologies that facilitate each of these two contrasting kinds of locomotion place constraints on the other. Most ground dwellers have great difficulty ascending steep surfaces, while climbers do not rise on the tips of the hind toes when running on the ground. Feet of forms using dense ground vegetation and of matrix climbers have their own characteristics but respectively tend to resemble the two kinds described above. Many lacertids show some intermediacy in limb morphology that reflects the conflicts and compromises of moving in more than one type of habitat.

The mode of locomotion of the immediate ancestor of modern lacertids is unknown but some degree of climbing is widespread in the primitive Palaeartic assemblage, even though a number of ground forms also exist. In the Armatured clade some climbing appears to be primitive and there are clear shifts: to specialised climbing on open surfaces, to matrixes, to using dense ground vegetation and finally to open ground.

INTRODUCTION

Locomotion of lizards has recently become a fashionable area of enquiry, particularly locomotor performance and its relationship to the ecology and morphology of the forms concerned (see for instance summary by Garland & Losos, 1994). While performance has often been studied in detail and comparative ecology is frequently well understood, morphology has often been limited to simple measurements, especially hind limb length. Little has been written in this context about foot morphology and how this affects locomotion, the main exceptions being for specialised feet such as the adhesive pads of anoles and geckoes (see for example Russell, 1976).

The 230 or so species of lacertid lizards occupy a wide range of

structural niches and, although they are morphologically quite uniform in many respects, exhibit substantial variation in limb proportions and structure of the feet, features that are often used in systematics (see for instance Boulenger, 1920, 1921). Informal observations suggest that limb and foot differences confer performance advantages in locomotion in particular habitats. This probable correlation between structure and function is explored here, and phylogenetic information used to get some idea of historical shifts in habitat and morphological features important in locomotion. As will become apparent the topic as a whole has many aspects and ramifications, all of which are susceptible to detailed and rigorous exploration. The intention of this article is to provide a preliminary overview that will allow such investigations to be placed in a broad context.

PHYLOGENETIC RELATIONSHIPS OF THE LACERTIDAE

The successively distant outgroups of the Lacertidae appear to be the 1. the Teiioidea, consisting of the Teiidae and the Gymnophthalmidae; 2. the Scincoidea consisting of the Scincidae, Cordylidae, Gerrhosauridae and probably the Xantusiidae; 3. the Anguimorpha (Estes, De Queiroz & Gauthier, 1988; Gauthier, pers. comm.). Phylogenetic hypotheses within the family based on morphology have been discussed elsewhere (Arnold, 1989a) and some of these relationships have been modified and extended on the basis of investigations using mitochondrial DNA sequence (Harris, Arnold & Thomas, submitted a). The phylogenies of particular groups of lacertids have also been explored (Arnold, 1989b, 1991, 1997; Harris, Arnold & Thomas, in press, submitted b–d).

DNA evidence suggests that the most basal branch within the family may comprise the sister genera *Gallotia* and *Psammodromus*. There may then be a dichotomy into two large clades (Fig. 1), one consisting of relatively primitive mainly west Palearctic taxa the other of forms that possess a combination of a complex supporting structure in the hemipenis, the armature, and a usually derived ulnar nerve condition (Arnold, 1989a). This Armatured clade contains *Omanosaura* and all the Afrotropical lacertids and some morphologically derived genera found in the arid parts of the Saharo-Eurasian region (Fig. 2). While relationships within the Armatured clade are reasonably well resolved, largely on the basis of morphology, those in the primitive west Palearctic assemblage are less clear. This group can be referred to as *Lacerta* and its allies, and consists of a paraphyletic *Lacerta* from which is derived *Algyroides* and *Podarcis*. The east Asian *Takydromus* may be sister taxon to *Lacerta* and its allies but the evidence for this is not strong and for present its relationships to this group and the Armatured clade are best regarded as unresolved. A number of assemblages within *Lacerta* and its allies can be tentatively recognised (Fig. 1).

1. *Lacerta agilis* group: *L. agilis*, *L. bilineata*, *L. media*, *L. pamphylica*, *L. schreiberi*, *L. strigata*, *L. trilineata*, *L. viridis*
2. *L. lepida* group: *L. lepida*, *L. pater*, *L. princeps* and *L. tangitana*. This assemblage has often been associated with the *L. agilis* group on the basis of morphology (Boulenger, 1920; Arnold, 1973, 1989a) and, although immunological data do not suggest such a relationship, DNA sequence does give some admittedly weak support.
3. *Lacerta vivipara*.
4. *Podarcis* and its relatives *Lacerta andreanskyi* and the sister species, *L. dugesii* and *L. perspicillata*.
5. *L. saxicola* group, consisting of *Lacerta saxicola* and generally similar 'archaeolacertas' in the Caucasus area including *L. chlorogaster*, *L. derjugini* and *L. praticola*. *L. brandtii* may be related to this assemblage.
6. Northwestern 'archaeolacertas'. *Lacerta bonnali* and the similar *L. aranica* and *L. aurelioi*, *L. horvathi*, *L. monticola*, *L. mosorensis*.
7. *Algyroides*
8. Southern 'archaeolacertas': *L. bedriagae*, *L. cappadocica*, *L. danfordi* group (*Lacerta anatolica*, *L. danfordi*, *L. oertzeni*), *L. bedriagae*, *L. graeca*, *L. kulzeri*, *L. laevis* and *L. oxycephala*. Unlike the other groupings, there is no evidence that these species constitute a clade.
9. *L. parva* and *L. fraasii*. Although morphology suggests these forms may be related to *Psammodromus* and *Gallotia* (Arnold, 1989a), mtDNA sequence provides no support for this arrangement, suggesting instead a relationship to *L. danfordi*.

STRUCTURAL NICHES OF LACERTID LIZARDS

Overview of lacertid structural niche space

The spatial niches that lacertid lizards occupy differ in both microclimate and their structural properties (Arnold 1973, 1987). The main structural variables include the nature, continuity and angle of the surfaces on which the lizards are active. Essentially the range of structural niches occupied forms a continuum. Many species occur on open ground that is flat or gently sloping. The substratum may be gravel or small stones, earth or sand or some mixture of these. Sandy substrata may be firm, soft, or even the mobile slip faces of dunes. In some situations the ground may be entirely bare but there is frequently cover of varying density and patchiness, consisting of grass or other herbaceous vegetation, bushlets or bushes. Lizards may take refuge among such plants when disturbed and, when cover is more continuous, some forms may spend much time in the interstices of vegetation near the ground. The interstices among pebbles or small rocks constituting scree may be occupied in a similar way. Some lacertids regularly climb high among vegetation including the twiggy matrixes of bushes and tree canopies, or flimsy plant matter such as herbs or high grass, over the top of which some forms may run. In contrast, many species climb in a different kind of situation characterised by continuous sloping or vertical surfaces, for instance rock faces, large boulders and tree boles and branches.

Some lacertid species specialise in a relatively narrow and homogeneous section of the habitat continuum occupied by the family as a whole. Others may spend time in more than one part, for instance, *Podarcis muralis* occurs on occasion on bare ground and among low vegetation but also climbs in hedges, on boulders and rock faces and even tree boles. Similarly, *Psammodromus algirus* is cursorial on the ground but also climbs in dense often spiny vegetation.

Structural habitats occupied by groups within the Lacertidae

Few quantitative data exist on differences in structural niche between lacertid taxa, but less formal information is available for many forms. This is briefly summarised here. Citations often refer to summaries rather than scattered primary sources. Information on many west Palearctic taxa can be found in Böhme, 1981, 1984, 1986; Arnold, 1987 and Arnold & Burton, 1978). The notes on lacertid habitats by R.H.R. Taylor cited below were made in northern Somalia in the 1930s and are deposited in the archives of the Reptile Amphibian Section, Natural History Museum, London.

Taxa are discussed in the approximate order in which they appear on the estimates of phylogeny in Figs. 1 and 2.

Primitive Palearctic forms

Psammodromus (SW Europe, NW Africa)

P. algirus often occurs on the ground in dry vegetated places but, as noted, also climbs extensively in bushes etc. The three species that constitute the *Psammodromus hispanicus* clade are strictly ground dwelling usually in places with patches of low dense vegetation in which they take refuge.

Gallotia (Canary islands)

All species occur extensively on the ground but also climb effectively.

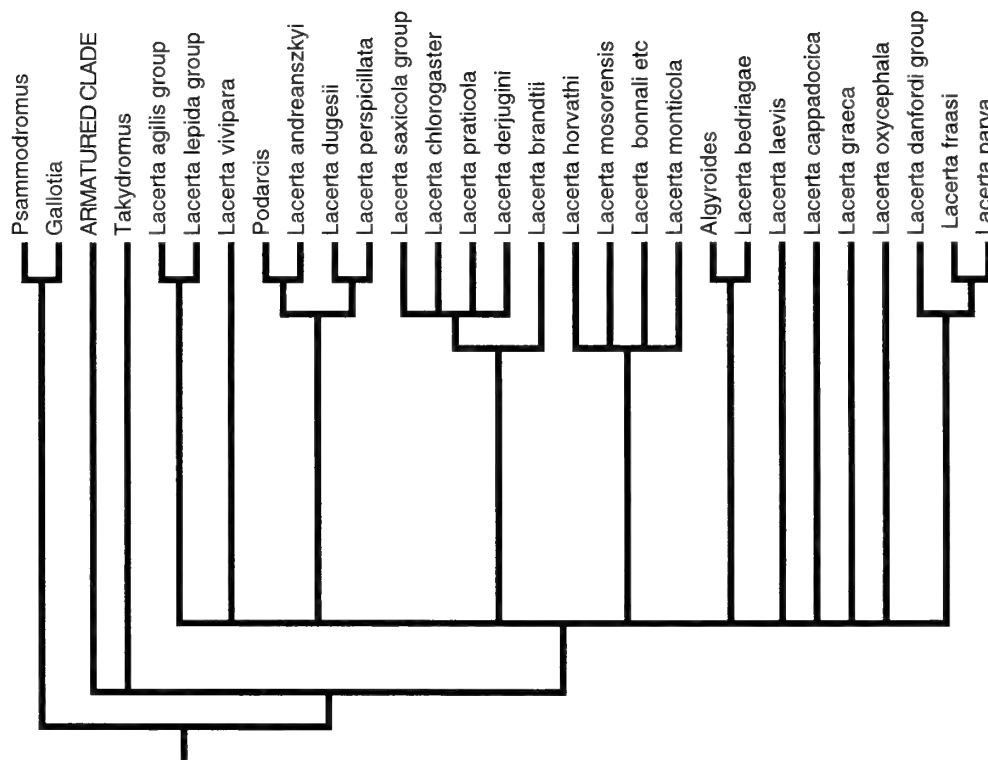


Fig. 1 Estimate of phylogeny for the Lacertidae. Relationships among many primitive Palaearctic taxa are largely unresolved. For contents of assemblages within the paraphyletic genus *Lacerta* see p. 65. As it is shown here the *Lacerta saxicola* group is not a clade.

Takydromus (E Asia).

This genus is made up of two sister clades, the subgenera *Takydromus* and *Platyplacopus*, with *T. amurensis* either basal to both or basal within the subgenus *Takydromus* (Arnold, 1997). Basal species in the genus *Takydromus* tend to be mainly ground dwelling but in each of the two constituent clades there is progressive shift to extensive climbing in flimsy vegetation such as grass and herbs. However, various morphological features likely to give performance advantage in such situations occur throughout the genus, which suggests that it may have been ancestrally climbing. If so there may have been a shift to a more ground-dwelling life mode and then two reversions to climbing (Arnold, 1997).

Lacerta agilis group (Europe, SW Asia)

Ground-dwelling and climbing especially in brambles (*Rubus*) and similar vegetation. *L. agilis* is more ground dwelling than the other species.

Lacerta lepida group (SW Europe, NW Africa, SW Asia)

Ground dwelling and climbing.

Lacerta vivipara (Europe eastwards to Sachalien)

Ground dwelling in and around herbaceous and heathland vegetation.

Podarcis (NW Africa, S and central Europe)

P. hispanica, and *P. muralis* are frequently active on the ground but also climb extensively, especially on rocky surfaces. Other species of *Podarcis* climb to varying extents but usually less than most populations of *P. hispanica* and *P. muralis*, spending a larger proportion of time on or close to the ground. This trend is particularly apparent in such forms as *Podarcis sicula*, *P. melisellensis* and especially *P. taurica*. *P. sicula* often runs considerable distances

across open areas. (Sources: Böhme, 1986; Arnold, 1987; Arnold & Burton, 1978; pers. obs.).

Lacerta andreanskyi (Atlas mountains of Morocco)

This high altitude species has been observed on flat or gently sloping areas of scree with many interstices and often some vegetation (Busack, 1987; pers. obs.). It is active on the irregular surfaces of such situations but also spends considerable time travelling through the spaces between the stones, something that can be confirmed by providing captives with a similar structural environment. The lizards pass through very narrow gaps and also often make sharp turns in confined spaces. *L. andreanskyi* make use of the thermal properties of the scree column to maintain their body temperature when the sun disappears. At such times, they retreat into the layer of stones immediately below the surface which still retains heat, descending further into more secure refuges when these cool (pers. obs.).

Lacerta dugesii and *L. perspicillata* (Madeira, NW Africa)

Both these species climb to a considerable extent on open usually rocky surfaces, a trend that is better developed in *L. perspicillata* (pers. obs.).

Lacerta saxicola group (Caucasus area and adjoining north Iran, Iraq and Turkey)

Lacerta saxicola and generally similar species in the Caucasus and adjoining areas occur especially on rocky exposures of various kinds. *L. chlorogaster* of north Iran etc is distinctive in being found in forest where it climbs on tree boles, while *L. praticola* and *L. derjugini* are mainly ground dwelling in mesic herbaceous situations (Bannikov *et al.*, 1977; Darevskii, 1967; Lantz & Cyren, 1947).

L. brandtii, which may possibly be related to the *L. saxicola* group, is basically ground-dwelling occurring in dry, open though

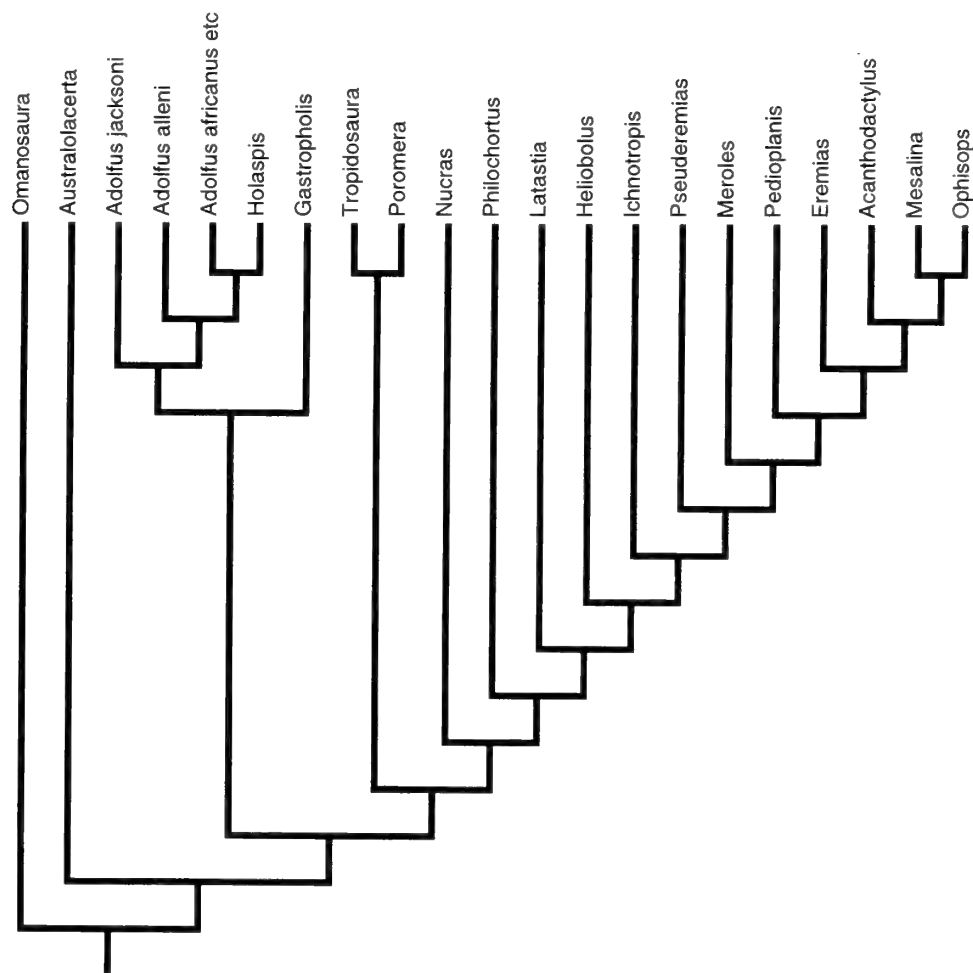


Fig. 2 Estimate of phylogeny for the Armatured clade of the Lacertidae. *Adolfus*, *Holaspis* and *Gastropholis* constitute the Equatorial African group.

sometimes broken situations with stones and sparse vegetation (Lantz & Cyren, 1939; S. C. Anderson, in press).

Northwestern archaeolacertas (NW Balkan area, S Austria, Pyrenees and Iberian Peninsula).

L. horvathi, *L. mosorensis* and *L. monticola* are rock dwelling in montane situations (Arnold, 1987) and the same is apparently true of *L. bonnali*, *L. aurelioli* and *L. aranica*.

Algyroides (S Europe)

This small genus appears to be primarily associated with woodland and woodland-edge habitats. In environments which have not been radically disturbed, *Algyroides* are frequently encountered among forest detritus such as fallen trunks, branches brushwood and litter. All four species may climb to some extent both in twiggy situations and on more continuous surfaces, including boles, branches and rocks. Such climbing is much more marked in *A. nigropunctatus* and *A. marchi* than in *A. fitzingeri* and *A. moreoticus* (Sources summarised by Arnold, 1987)

Southern 'archaeolacertas' (N and E Mediterranean area, east to N Iraq).

All species climb substantially although to varying extents. Climbing usually takes place on rocky surfaces (Arnold, 1973, 1987) but *L. laevis* sometimes also occurs on tree boles (Zinner, 1967). The most scansorial species is *L. oxycephala*. (Sources: Böhme, 1984; Arnold, 1987)

Lacerta parva and *L. fraasii* (Lebanon, E. Turkey, NW Iran, Transcaucasus)

Both species are basically ground-dwelling occurring in dry, open though sometimes broken situations with stones and sparse vegetation. (Wettstein, 1928; Peters, 1962; S. C. Anderson, in press; In den Bosch, 1994)

Members of the Armatured clade

Omanosaura (E Arabia)

Both *O. cyanura* and *O. jayakari* climb on rocky surfaces, but the latter species also spends time on open ground and occasionally even climbs in low trees (Arnold & Gallagher, 1977; pers. obs.).

Australolacerta (South Africa)

Both *A. australis* and *A. rupicola* occur on rocky surfaces and climb to a considerable extent (FitzSimons, 1943; De Villiers, Branch & Baard, 1983; Branch, 1988).

Adolfus (Forest regions of east and central Africa)

A. jacksoni, *A. africanus* and *A. vauereselli* are all essentially woodland species that often climb on fallen timber and sometimes standing trees as well. They also forage on the ground and *A. africanus* at least may climb twiggy and herbaceous plants (pers. obs.). *A. alleni* is a high altitude species occurring above the tree line in moorland situations where it lives on the ground, taking refuge in

dense tussocks of coarse and spiny vegetation. (Sources summarised by Arnold, 1989b).

Holaspis (Forest regions of tropical Africa and some adjoining savanna areas.)

The single species, *H. guentheri*, occurs on the trunks and branches of standing trees, often at some height, and does not usually come to the ground. It appears to spend much more time on steep and vertical surfaces than any other lacertid and also often investigates narrow crevices in wood and under bark. *Holaspis* is unique within its family in being able to glide from tree to tree. (Sources summarised by Arnold, 1989b).

Gastropholis (Forested areas of tropical Africa)

The little information available suggests the four species of this genus are arboreal and essentially canopy forms, spending much of their active time among twiggy vegetation. (Sources summarised by Arnold, 1989b).

Tropidosaura (S Africa).

These are ground-dwelling species in mountain areas and are usually encountered in and around dense grassy or bushy vegetation. Such behaviour occurs in the most basal species of the clade, *T. montana*, and may be primitive for the genus, all members of which lack a collar beneath the throat and have large imbricate, pointed, keeled dorsals, features usually associated with use of dense vegetation as cover (Arnold, 1973). Two of the four species, *T. gularis* and *T. cottrelli*, also climb on rock surfaces to a limited extent. If this is a derived condition it is likely to have developed twice. (Sources: Branch, 1988, pers. comm.; pers. obs.).

Poromera (Forested areas of W Africa from Gabon to Cameroun.) Occurs on the forest floor and on fallen logs (M. Largen pers. comm.; Freyhoff, 1994) and also climbs in grassy vegetation (Perret and Mertens, 1957).

Nucras (E and southern Africa)

Ground dwelling especially in mesic and arid savannah often on sandy soils. Many species are secretive and only seen after rain, although *N. tessellata* is active at high temperatures. *N. lalandei* occurs under stones and in long grass. (Sources: Branch, 1988, pers. comm.; FitzSimons, 1943; Pianka, 1986).

Philochortus (NE Africa; isolated localities in and around the Sahara desert)

Ground dwelling in dry places on sandy and stony soils often with grass and bushes (R.H.R. Taylor, notes). Matschie (1893) recorded *P. neumanni* from high grass. *Philochortus* possesses morphological features that have independently evolved in the lacertid genera that climb in grassy vegetation, *Takydromus* and *Poromera*, and appear to confer performance advantage in that situation; these features include, enlarged vertebral scales with a coarse microornamentation of anastomosing ridges, a long tail and sagittally expanded neural spines (Arnold, 1997).

Latastia (SW Arabia, NE and E Africa, westwards through the Sahel)

Ground dwelling in dry places with sparse vegetation (Dunger, 1967; R.H.R. Taylor, notes; J. Vindum, pers. comm.).

Heliobolus East and tropical southern Africa, Sahel etc.)

Ground dwelling in dry places. *H. lugubris* occurs on sparsely vegetated compacted sandy plains and in bush veldt (Branch, 1988; FitzSimons, 1943; R.H.R. Taylor, notes).

Ichnotropis (Tropical southern Africa)

Ground dwelling in arid and mesic savannah often with sandy soil (Branch, 1988; FitzSimons, 1943).

Pseuderemias (NE Africa)

On dry ground ranging from firm, rocky substrata to dunes (Gans & Laurent, 1965; R.H.R. Taylor, notes).

Meroles (SW Africa)

The evolution of this arid ground-dwelling clade is discussed elsewhere (Arnold, 1990, 1991) and habitat differences between the species summarised (Arnold, 1995). Most species occur on sandy substrata but a succession of shifts to increasingly extreme environments occur along the main lineage of the phylogeny. The sequence is: relatively firm surfaces (*M. knoxii* and *M. suborbitalis*), vegetated hummocks separated by open areas of soft sand (*M. reticulatus*), areas of looser sand and more open vegetation (the subgenus *Saurites*, consisting of *M. ctenodactylus*, *M. micropholidota* and *M. cuneirostris*), bare slip faces of dunes (*M. anchietae*). Overall the trend is towards softer substrata and more open situations.

Pedioplanis (S Africa and Namibia)

Ground dwelling in dry usually open areas on firm substrata such as flat and sloping rocky areas, gravel, hard soils, sandy plains and grassy hillsides (FitzSimons, 1943, Branch, 1988).

Eremias (Palearctic Asia and adjoining regions)

Ground dwelling in dry situations and habitats occupied by members of the genus include firm soil, firm sand, loess and aeolian sand; the latter habitat may have been entered twice (S. C. Anderson, in press; Minton, 1966; Shcherbak, 1974; Smith, 1935).

Acanthodactylus (N Africa, Middle east to NW India)

Ground dwelling in open dry situations, usually on light soils or sand. Within this general environment, there is considerable variation in microhabitat among species. Many relatively primitive forms usually occur on fairly firm substrata with at least scattered vegetation and the *A. pardalis* group is found on loess soils. Perhaps three lineages appear to have shifted into aeolian sand habitats, although they may sometimes have partially reverted to firmer ground: 1. *A. grandis* of Syria, Iraq and adjoining regions; 2. the *A. scutellatus* clade of North Africa and northern Arabia of which *A. longipes* is found in the softest most open situations (Perez Mellado, 1992; S. Baha el Din, pers. comm.); 3. a clade ranging from Arabia to NW India consisting of *A. cantoris* and its immediate relatives, among which *A. haasi* is distinctive in often climbing in bushes. (Sources: S. C. Anderson, in press; Arnold, 1983, 1984, 1986a; Dunger, 1967; Ross, 1989, Mellado & Olmedo, 1991; Perez Mellado, 1992)

Mesalina (N Africa, Arabia, Middle East to NW India)

Ground dwelling in dry, open situations on firm substrata. Most species tend to occur on compact often sandy soils but members of the clade containing *M. guttulata* and *M. watsonana* are often found in gravelly, stony or rocky situations. (S. C. Anderson, in press; Arnold, 1984; Minton, 1966; Perez Mellado, 1992; Ross, 1989).

Mesalina ercolinii (Lanza and Poggesi, 1975) is only known from a single specimen collected in central Somalia. It was initially assigned to *Eremias* but is probably part of the *Mesalina* clade (Arnold, Lanza *et al.*, in press). The sole individual was collected in a savannah habitat but there are no direct observations on its life mode.

Ophisops (Coastal regions of N Africa; Turkey and Middle east to India and Sri Lanka)

Ground-dwelling, usually in generally dry situations often on sandy soils which may bear grass or patches of dense vegetation. (S. C. Anderson, in press; Minton, 1966; Schätti & Gasperetti, 1994; Smith, 1935). In Sri Lanka, *O. leshchenaultii* occurs in more open dune areas (T. B. Karunaratne, pers. comm.).

Evolutionary change in structural niche

Because of the range of habitats occupied by lacertids and the wide variation in degree of climbing they exhibit, it is very difficult to assign species to a simple set of well defined structural niche states. However there are a number of broad categories that can be recognised, even though there is considerable variation within these and some species may be assignable to more than one.

G – Ground dwelling in open areas.

V – Ground dwelling and spending considerable time in situations where movement may be restricted, such as dense grassy or twiggy vegetation and the analogous interstices of scree etc.

M – Climbing regularly in vegetation where the lizard tends to progress through or over a matrix of twigs, leaves or grass.

C – Climbing regularly on more or less continuous largely open surfaces, such as rock faces and tree boles.

The immediate outgroup of the Lacertidae, the Teiioidea, is almost entirely ground dwelling and this appears to be the primitive situation for the next most closely related outgroups, the Scincomorpha and the Anguimorpha. However, while this suggests the earliest lacertids may have been ground dwelling too, this is not necessarily so for the immediate ancestor of surviving species.

Unfortunately, the overall history of structural niche within the family is difficult to assess because basal relationships within the primitive Palaearctic assemblage are not fully resolved. However many of the component taxonomic units of this assemblage include species that climb to some extent and often, taking these units on their own and considering all evidence, it is more parsimonious to regard some degree of climbing as the primitive situation relative to a more ground-dwelling life mode. This is true for instance in *Takydromus*, *Podarcis* and its relatives and the *Gallotia-Psammodromus* clade.

Whether it is assumed ground dwelling or climbing is primitive for the surviving members of the family, numerous transitions between different kinds of structural habitats have to be postulated. Even within *Takydromus* there may have been a shift from climbing to a more ground dwelling way of life and then two independent shifts back to climbing (p. 66).

When some degree of climbing versus ground-dwelling is plotted on the general pattern of relationships assumed here for the primitive Palaearctic assemblage, it is more parsimonious to assume some degree of climbing as the initial state, with multiple shift to life mainly on the ground, either in and around dense vegetation or in more open situations. However, this assumption is not very robust, as assuming a ground-dwelling ancestry in *Takydromus* rather than a climbing one makes the ancestral condition uncertain.

If a partially climbing ancestry is accepted, there must have been, within the primitive Palaearctic assemblage, shifts to more specialised climbing on continuous surfaces (C) in such forms as *Lacerta oxycephala* and *L. perspicillata*, and to specialised climbing in vegetation matrices (M) in *Takydromus*. *L. vivipara* would have become ground-dwelling in dense vegetation (V) and this would have occurred separately in *L. derjugini* and *L. praticola* within the *L. saxicola* group. The *L. parva*-*L. fraasii* clade and *L. brandtii* would have separately entered more open ground situations (G), and the *Psammodromus hispanicus* clade occupied often intermediate habitats (G and V).

The history of alteration of structural niche is clearer in the Armatured clade where phylogenetic structure is more apparent. Here, some climbing on continuous surfaces appears to have been the primitive situation. In the Equatorial African group there was one shift to specialised open surface climbing (C) in *Holaspis*, one to matrix climbing (M) in canopy in *Gastropholis* and one to using

ground vegetation (V) in *Adolfus alleni*. In the main lineage of the Armatured clade, parsimony supports a shift to more extensive ground dwelling in the ancestor of the clade made up of *Tropidosaura* and its advanced relatives with subsequent shift to more open habitats. At the base of this clade there would have been partial shifts to other modes: a reversion to a small degree of climbing in two species of *Tropidosaura*, and to making some use of vegetable matrixes in *Poromera* and perhaps *Philochortus*. Alternatively, *Tropidosaura*, and *Nucras* and its advanced relatives may have become ground-dwelling independently.

Overall there may have been a minimum of nine shifts to ground dwelling although only about three were into really open situations (G), five to climbing in vegetable matrixes and others to specialised climbing on continuous surfaces. Among members of the Armatured clade, there were multiple shifts on to soft sandy substrata: at least one each in *Pseuderemias*, *Meroles* and *Eremias* and perhaps three in *Acanthodactylus*.

Reversals in structural niche within the Lacertidae are less obvious, although morphology suggests this may have happened in *Takydromus*, *Acanthodactylus* and *Meroles*.

MORPHOLOGY

Body proportions and vertebral number

Bodies of lacertids vary in their proportions, especially in the extent of elongation, and change in number of presacral vertebrae is often associated with this. The number shows some individual variation in most species and females usually have more presacral vertebrae than males (often about one on average but sometimes two). Typically there are eight nuchal vertebrae and five sternal vertebrae with ribs attached to the sternum, but the number of more posterior presacral vertebrae varies considerably. There may be as few as ten in some *Pseuderemias* and *Acanthodactylus* and as many as twenty in some female *Nucras lalandei*, making the total presacral range for the family 23 to 33 vertebrae.

Fairly elevated presacral counts also occur in *Lacerta agilis*, *Lacerta parva* and *L. fraasii*, some members of the *L. saxicola* group, *L. andreanskyi*, *L. graeca*, *Adolfus alleni* and *Gastropholis* (Arnold, 1973, 1989b). Females of these forms often have a total of 29 presacral vertebrae while *Gastropholis* frequently possesses 30. Relatively low presacral counts of 24 to 26 in females are usual in the more derived members of the Armatured clade including *Philochortus* and its sister group; they also occur sporadically elsewhere.

Presacral vertebral count shows some correlation with habitat. Forms where it is high include those that spend time in dense vegetation, such as *Lacerta agilis*, *Adolfus alleni*, *Gastropholis*, and *Nucras lalandei* while numbers are particularly low in species regularly occurring in open situations. This may be related to the amount of body flexibility necessary to negotiate habitats where possible paths are often tortuous and ones which are unimpeded. *L. andreanskyi* which may spend considerable time in the interstices of scree also has high counts. However any association between vertebral number and the functional demands of habitat is imprecise, as high counts also occur in forms that often live in open rocky situations, such as *Lacerta graeca* and members of the *L. saxicola* group.

Sexual variation in presacral vertebral count is absent in *Gallotia*, and independently lost three times in *Acanthodactylus*: in *A. bedriagai*, in *A. schmidtii* populations in the United Arab Emirates, and in the *A. scutellatus* group. All these cases appear to involve reduction in female presacral number, except *A. bedriagai* where

there may have been an increase in male counts. In several ground dwellers in dense vegetation, females have on average two more presacral vertebrae than males. Included here are the *Psammodromus hispanicus* group, *Lacerta agilis*, *L. derjugini*, *L. praticola*? and *Adolfus alleni*. Number of abdominal vertebrae appears also to be influenced by relative clutch mass (Bauwens, Barbadillo & Gonzalez, 1997).

Relative tail length

Because caudal autotomy and partial regeneration are frequent, adequate data on the relative length of intact tails in adult lacertids are not easy to collect. In most adult lacertids, intact tails vary in length from about 1.7 to about 2.7 times the length of the head and body. However, they are often over three times as long in many *Takydromus*, *Psammodromus algirus*, *Gastropholis*, *Philochortus neumanni* and *P. hardeggeri*, *Latastia longicaudata*, *Pseuderemias mucronata* and *P. striata*. The longest tails occur in *Takydromus sauteri*, where they

may be four times as long as the head and body, and in some *T. sexlineatus*, where the tail is five times as long. Tails are particularly short, being around 1.4 to 1.6 times the head plus body length, in *Holaspis*, *Eremias argus*, *E. przewalskii*, *E. quadrifrons*, *Acanthodactylus tristrami*, *A. robustus* and *Mesalina rubropunctata*. In *Meroles anchietae* and *Eremias arguta* the figure falls to about 1.

Very long and very short tails are both derived conditions within the Lacertidae that have arisen several times. Very long tails are frequent in forms that climb in vegetation matrixes, such as *Takydromus*, *Gastropholis*, *Psammodromus algirus* and perhaps the species of *Philochortus* mentioned. In at least the first two genera, the tail is used to maintain position among stems and twigs (Arnold, 1989b, 1997) and, in general, appears to spread weight in flimsy vegetation. This occurs in some *Takydromus*, such as *T. sexlineatus*, when they run across the top of high grass, a situation where the tail may perhaps also contribute thrust through lateral sinusoidal motion. In the two main clades of *Takydromus* (Arnold, 1997) there are

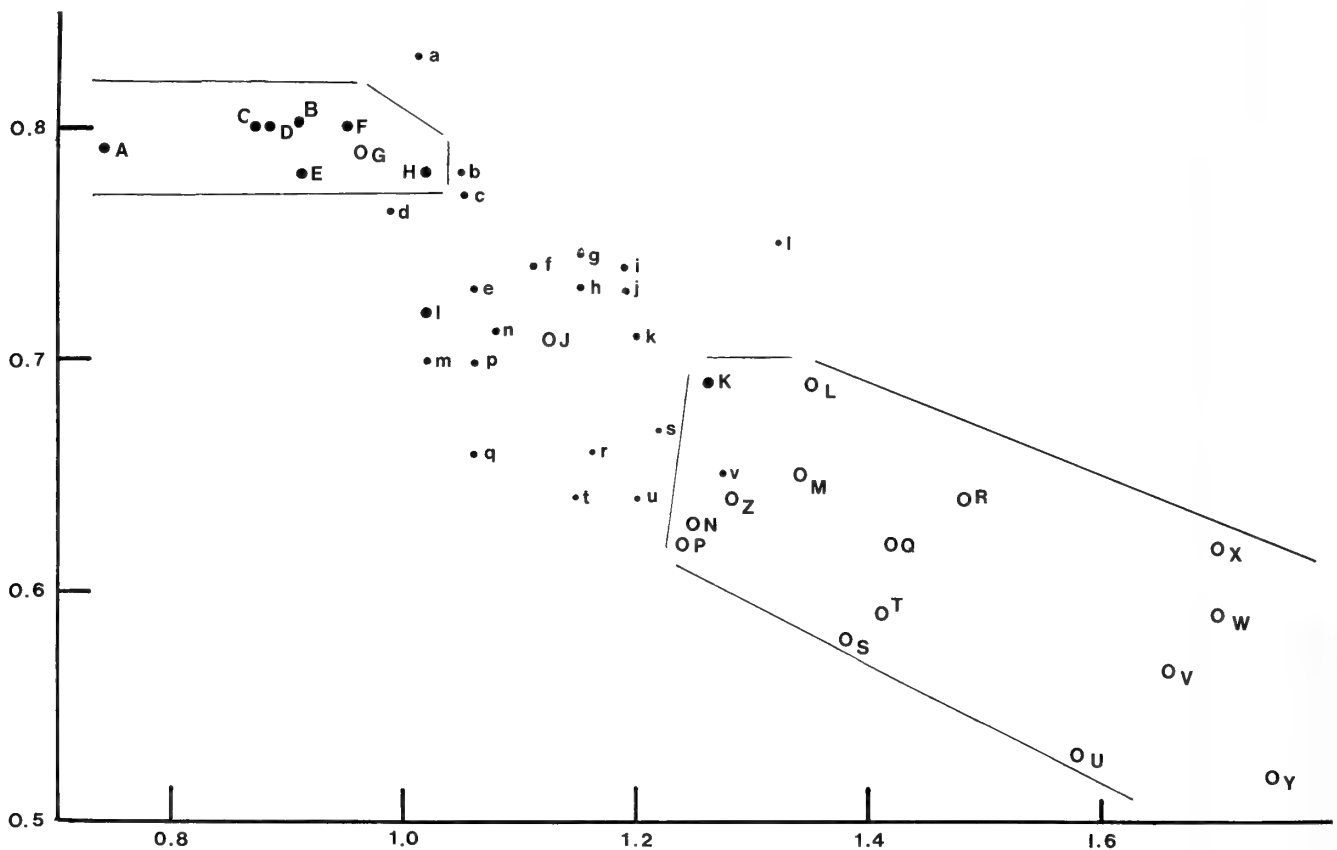


Fig. 3 Limb proportions of lacertid lizards based on data in Table 1; sexes pooled. Vertical axis: FL/HL – Forelimb span/hindlimb span. Horizontal axis: HL/SV – Hindlimb span/snout-vent distance ● – More primitive ground dwellers; ○ – Ground dwellers of the clade consisting of *Philochortus* and its sister group; • – forms that regularly climb to some extent. Ground dwellers using dense vegetation (upper box), also included is *Lacerta andreanszkyi* which often occurs in the interstices of scree: A. *Nucras lalandei*, B. *Lacerta vivipara*, C. *Lacerta andreanszkyi*, D. *Tropidosaura montana*, E. *Adolfus alleni*, F. *Lacerta agilis*, G. *Mesalina ercolinii* and H. *Takydromus amurensis*. Ground dwelling forms of generally open situations (lower box): K. *Psammodromus hispanicus*, L. *Eremias persica*, M. *Ichnotropis capensis*, N. *Philochortus intermedius*, P. *Latastia longicaudata*, Q. *Ophisops schlueteri*, R. *Pedioplanis lineocellata*, S. *Acanthodactylus schmidtii*, T. *Acanthodactylus scutellatus*, U. *Heliobolus lugubris*, V. *Meroles reticulatus*, W. *Meroles ctenodactylus*, X. *Meroles anchietae*, Y. *Pseuderemias mucronata*, Z. *Mesalina balfouri*. Ground dwellers that probably fall between the above two situations: I. *Nucras boulengeri*, J. *Mesalina* species A, SW Arabia (Arnold, 1986b). Forms known to climb on continuous surfaces and in vegetation matrixes; overall, q–u appear to climb least: a. *Holaspis guentheri*, b. *Takydromus septentrionalis*, c. *Gastropholis vittata*, d. *Gastropholis echinata*, e. *Lacerta perspicillata*, f. *Lacerta pater*, g. *Lacerta oxycephala*, h. *Lacerta mosorensis*, i. *Lacerta jakakari*, j. *Algyroides nigropunctatus*, k. *Lacerta bedriagae*, l. *Poromera fordii*, m. *Podarcis hispanica*, n. *Podarcis muralis*, p. *Lacerta viridis*, q. *Podarcis melisellensis*, r. *Podarcis sicula*, s. *Lacerta laevis*, t. *Podarcis peloponnesiaca*, u. *Lacerta trilineata*, v. *Psammodromus algirus*.

independent shifts to increased climbing in vegetation and this is associated with greater tail length.

Apart from locomotory considerations, tail length in lacertids may be influenced by different patterns of predation associated with particular kinds of habitat. It has been suggested that long tails are more likely to be effective in deflecting the attack of ambushing predators and so would be expected in lizards that often hunt actively in complex spatial habitats where such predators might hide; in contrast it is predicted that more passively hunting lizards in open situations would have short tails. Some indications of such an association has been suggested for Southern African desert lacertids (Huey & Pianka, 1981) and, taking the family as a whole, nearly all species with very short tails are ground-dwellers in open situations. The only exception is the aberrant tree-dwelling and gliding *Holaspis*.

The pattern of tail growth varies in lacertids. Relative tail length often increases with body size, for instance in *L. dugesii*, *L. vivipara* and *L. jayakari*, but decreases in *Acanthodactylus scutellatus*. In *Lacerta lepida* relative tail length rises steeply at first but subsequently levels out and eventually tends to fall and a similar growth pattern appears to be present in *L. trilineata*

Limb proportions and structural niche

Limbs of lacertids are often measured individually (see for instance Darevskii, 1967), but in intact animals it is difficult to determine a reliable reference point for the base of the limb which is situated in soft tissue. Because of this it is easiest to measure the total span of a pair of limbs when fully outstretched, from the tip of the longest digit on one side to that on the other. Fore and hind limb spans can then be compared with each other and with the total length of the head and body measured from the tip of the snout to the vent. The latter is of course not an absolute criterion for comparison. As already noted, presacral vertebral number varies between species and sexes, and this is also true of the size of the head relative to the body; both these factors affect body length.

Estimates of hind leg span in terms of head and body length, and the ratio of foreleg and hind leg spans, are given for a wide variety of lacertids in Table 1 and the relative distribution of selected species in terms of these parameters is shown in Fig. 3. In the latter, the species all fall in a restricted area of the diagram. Not only do no forms exist where the forelimbs are longer than the hindlimbs but there is a broad correlation between hindlimb length and the relative length of the forelimbs: in cases where hindlimbs are comparatively short, forelimbs tend to approach them in length, but where hindlimb span is large, forelimb span is relatively much smaller. It follows from this that the overall range of hindlimb span in terms of body length is much greater than that of the forelimbs: for the former, the highest ratio is about 2.8 times the lowest compared with less than 1.5 times for the latter.

The kind of structural habitats species occupy correlates quite clearly with limb proportions. Ground dwelling forms that often occur in dense vegetation or litter have short, subequal limbs and this is true of *Lacerta andreanskyi* which appears to often spend time in the confining interstices of scree. Climbing forms are similar in proportion of the limb pairs although their legs are usually rather longer and this pattern is found both in climbers on open surfaces such as *Holaspis* and in forms from vegetation matrixes such as *Gastropholis* and *Takydromus*. Limbs are longer still in climbing forms that also utilise less steep surfaces quite extensively, such as *Lacerta oxycephala*. Forms which climb considerably but also run in more or less horizontal situations have even longer and less equal limb pairs. Species that scarcely climb and occupy open ground habitats all have very long hind legs and short front ones. This is best

Table 1 Limb proportions of lacertid lizards. HL/SV – Hindlimb span/snout–vent distance; FL/HL – Forelimb span/hindlimb span; m – male, f – female.

Species and sample size	HL/SV		FL/HL	
	Male	Female	Male	Female
Takydromus amurensis (6m,4f)	1.02	1.03	.78	.77
Takydromus septentrionalis (11m,10f)	1.08	1.02	.78	.77
Gallotia atlantica (3m,3f)	1.25	1.13	.69	.70
Gallotia g. caesaris (3m,3f)	1.34	1.26	.69	.69
Psammmodromus algirus (6m,6f)	1.30	1.24	.65	.64
Psammmodromus hispanicus (7m,10f)	1.30	1.23	.68	.70
Lacerta vivipara (10m,10f)	0.99	0.81	.82	.78
Lacerta agilis bosnica (10m,10f)	1.01	0.88	.80	.80
Lacerta viridis (10m,10f)	1.09	1.03	.70	.69
Lacerta trilineata (9m,10f)	1.20	1.20	.64+	.64
Lacerta lepida (5m,6f)	1.14	1.04	.71	.72
Lacerta pater (7m,5f)	1.11	1.10	.74	.73
Lacerta andreanskyi (1m,4f)	0.96	0.78	.73	.86
Lacerta laevis (10m,10f)	1.26	1.17	.66	.67
Lacerta danfordi (7m,5f)	1.27	1.16	.67	.68
Lacerta bedriagae (8m,13f)	1.23	1.16	.71	.70
Lacerta mosorensis 10m,10f)	1.17	1.1	2.71	.74
Lacerta oxycephala (10m,10f)	1.17	1.13	.74	.73
Algyroides nigropunctatus (10m,7f)	1.25	1.12	.71	.74
Lacerta perspicillata (9m,11f)	1.13	1.00	.72	.74
Podarcis hispanica (9m,6f)	1.18	1.05	.69	.71
Podarcis m. fiumana (10m,10f)	1.14	0.99	.65	.67
Podarcis muralis (10m,10f)	1.12	1.03	.71	.71
Podarcis s. campestris 10m,10f)	1.20	1.12	.66	.65
Podarcis peloponnesiaca (19m,11f)	1.20	1.09	.63	.64
Lacerta jayakari (7m,9f)	1.20	1.18	.75	.72
Adolfus alleni (9m,7f)	0.94	0.87	.77	.78
Holaspis guentheri (3m,4f)	1.01	1.01	.85	.80
Gastropholis echinata (4m)	1.05		.77	
Gastropholis tropidopholis (1f)		1.16		.74
Gastropholis vittata (1m,1f)	1.01	0.94	.76	.78
Gastropholis prasina (1m)	1.04		.77	
Tropidosaura montana (3m)	0.88		.8	
Tropidosaura gularis (1m,1f)	1.15	0.97	.72	.77
Tropidosaura essexi (2m)	1.05		.71	
Tropidosaura cottrelli (1m)	1.06		.77	
Poromera fordii (3m,3f)	1.35	1.28	.75	.74
Nucras boulengeri (7m,7f)	1.03	1.01	.72	.71
Nucras lalandei (4m,1f)	0.82	0.67	.79	.79
Philochortus intermedius (5m,4f)	1.34	1.16	.60	.66
Latastia longicaudata (10m,6f)	1.29	1.18	.61	.63
Heliobolus lugubris (7m,4f)	1.58	1.57	.53	.53
Ichnotropis capensis (9m,5f)	1.38	1.29	.64	.65
Pseuderemias mucronata (12m,6f)	1.81	1.68	.51	.53
Meroles reticulatus (1m,4f)	1.73	1.58	.60	.57
Meroles ctenodactylus (3m,1f)	1.7	1.7	.60	.58
Meroles cuneirostris (1f)		1.61		.57
Meroles anchietae (2m,1f)	1.74	1.66	.62	.62
Pedioplanis lineocellata (4m,4f)	1.49	1.46	.64	.64
Eremias persica (3m,5f)	1.38	1.32	.68	.69
Acanthodactylus schmidtii (12m,10f)	1.37	1.38	.58	.58
Acanthodactylus scutellatus (10m,3f)	1.42	1.41	.58	.59
Mesalina balfouri (6m,4f)	1.34	1.22	.63	.64
Mesalina 'A', SW Arabia (2m,4f)	1.20	1.04	.69	.72
Mesalina ercolini (1f)		0.96		.79
Ophisops e. schlueteri (5m,6f)	1.51	1.32	.62	.61

developed in *Latastia* and its sister group in the Armatured clade and reaches its extreme in forms like *Heliobolus lugubris*, *Pseuderemias mucronata* and the most derived species of *Meroles*. Among the species investigated here, advanced armatured ground dwellers are approached most closely in limb proportion within the primitive Palaearctic assemblage by *Psammmodromus*, the species of *Podarcis* that climb least, and by *Lacerta trilineata*.

Because of their correlation with spatial niche, limb proportions

can be used to generate hypotheses about the habitats and locomotory modes of species where these are uninvestigated or incompletely so. Thus the one known specimen of *Mesalina ercolinii* occurs in the area of Fig. 3 mainly occupied by ground dwelling forms using dense vegetation, an exceptional habitat for an advanced armatured lacertid. The African *Poromera fordii* has many morphological resemblances to the east Asian grass lizards, *Takydromus*, that seem to be related to climbing in vegetation (Arnold, 1997) but, although the limb pairs of *Poromera* are not very disparate in length, as expected in a climber, they are distinctly longer than in *Takydromus* and other scansorial species. This suggests a locomotory difference between the two genera and perhaps indicates that, although *Poromera* does climb in vegetation, it is also frequently active in open situations, for instance it may run on the ground more extensively than *Takydromus*.

Sexual dimorphism in limb length

It will be seen from Table 1 that there is sexual variation in relative length of the hindlimbs, which nearly always appear to be shorter in females. In most cases the apparent difference is slight, but in a number of taxa, it is substantial, the mean adult male hindlimb span in terms of body length sometimes being as much as 12% more than that of females. Marked sexual difference occurs in, among others, *Psammodromus hispanicus*, *Lacerta agilis*, *L. lepida*, *L. andreanszkyi*, *L. laevis*, *L. danfordi*, *Algyroides nigropunctatus*, *Lacerta perspicillata*, *Adolfus alleni*, *Podarcis*, *Philochortus intermedius*, *Latastia longicaudata*, *Pseuderemias mucronata*, *Mesalina* and *Ophisops*. In many cases, reduced hind limb span in females is associated with raised forelimb/hindlimb ratio, so sexual differences

within species follow the general trend among species (Fig. 4). There appear however to be exceptions to this regularity, for instance in *Lacerta vivipara*.

The sporadic distribution of marked sexual difference in limb length indicates that it has arisen a number of times. There are also phylogenetic indications that sexual dimorphism may have often developed by change in limb proportions of the females rather than the males.

The clear relationship among species between limb proportions and the kind of spatial niche occupied suggests that intraspecific sexual differences in limb length may reflect differences between the sexes in microhabitat, although these do not seem to have been systematically looked for. In some cases limb dimorphism is often associated with differences in dorsal colouring and pattern that may possibly be related to the problems of camouflage in different environmental situations. Thus, in *Podarcis*, females not only have shorter hind legs but are more obviously longitudinally striped than males, a pattern that may be more cryptic in more vegetated situations.

Many forms with sexual dimorphism in limb length also show dimorphism in head size which is probably associated with male combat for territory and females, large heads presumably conferring advantage in this situation. It might be thought that large limbs would also be beneficial in this context, but the relationship between head and limb size is not precise and some forms where the males have large heads show little apparent limb difference between the sexes, for instance *Lacerta viridis* and *L. trilineata*. The fact that sexual dimorphism in limb proportions may be produced by devia

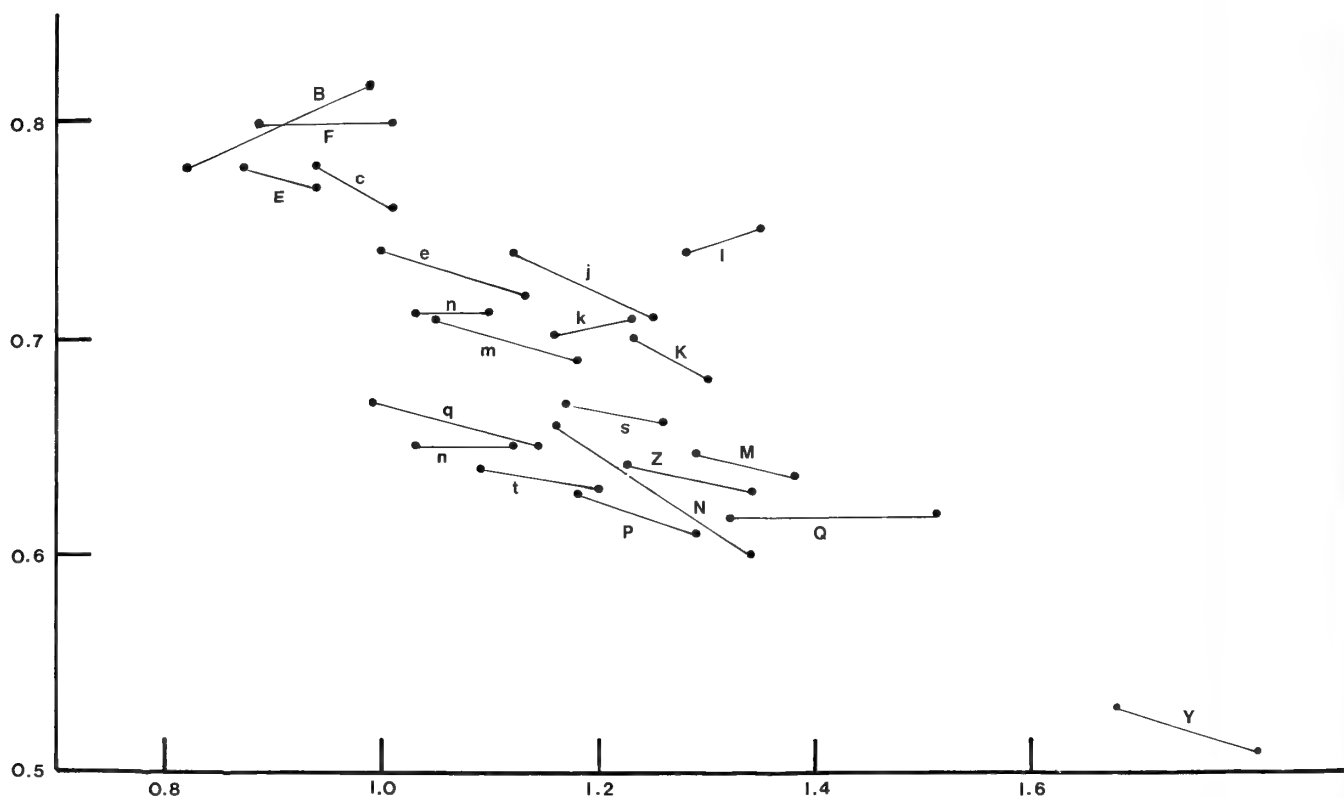


Fig. 4 Sexual differences in limb proportions in selected dimorphic species. Vertical axis: FL/HL - Forelimb span/hindlimb span. Horizontal axis: HL/SV - Hindlimb span/snout-vent distance. Lines join means for the two sexes, females are always to the left. Letters refer to species as indicated in the caption of Fig. 3. Sexual differences in hindlimb length are often large, compared with mean species differences; females often have more equal limb pairs than males.

tion to shorter limbs in females rather than increase in limb size in males also militates against this explanation.

It might be thought that the relatively low hindlimb/snout-vent ratios of many female lacertids is a result of their usually higher average number of presacral vertebrae than males (Arnold, 1973, 1989a), something that tends to produce a proportionally longer body. However, while this may be a partial cause of low ratios, it is not a total explanation. In *Gallotia atlantica* and *G. galloti caesaris*, for instance, where virtually all individuals have 26 presacral vertebrae without sexual difference, females still have relatively shorter hind legs.

Relative proportions of femur and tibia

Measurements of the femur and tibia on dry skeletons and cleared and stained preparations of single individuals of a wide range of lacertid species show considerable variation. The approximate ratio of tibia length to femur length is generally low in members of the primitive Palaearctic assemblage and more basal members of the Armatured clade where it ranges from about 0.73–0.87. The ratio is particularly low, about 0.73–0.77, in such climbing forms as *Lacerta oxycephala*, *L. bedriagae*, *L. horvathi*, *L. perspicillata*, *L. mosorensis* and *Holaspis guentheri*.

Generally rather higher ratios, 0.76–0.87 occur in *Takydromus septentrionalis*, *Lacerta agilis*, *L. vivipara*, *Psammodromus algirus*, *Lacerta schreiberi*, *L. pater*, *L. chlorogaster*, *L. monticola*, *L. dugesii*, *Podarcis bocagei*, *P. muralis*, *P. sicula*, *Adolfus jacksoni* and *Poromera fordii*.

Ratios are higher still, 0.88–1.00, in *Psammodromus hispanicus*, *Lacerta trilineata*, *Adolfus alleni* and the clade containing more advanced members of the Armatured group, namely *Nucras* and its sister group, most of which are largely or entirely ground dwelling in open places. Included here are *Poromera fordii*, *Nucras boulengeri*, *N. lalandei*, *Philochortus spinalis*, *Latastia longicaudata*, *Heliobolus lugubris*, *Ichnotropis squamulosa*, *Pseuderemias brenneri*, *Meroles knoxii*, *M. ctenodactylus*, *Eremias arguta*, *Acanthodactylus erythrurus*, *A. boskianus*, *Mesalina rubropunctata*, *Ophisops elegans*.

Patterns of limb growth

Like patterns of tail growth, the way in which the length of hind limbs relative to that of the head and body changes during growth from hatching to maturity is extremely varied. In such forms as *Takydromus septentrionalis* and *Lacerta oxycephala* the hindlimbs retain much the same relative size, while in *Acanthodactylus scutellatus* and *A. schmidtii* they show distinct reduction, for instance growing only 90% as fast as the head and body length in *A. schmidtii*. In *Podarcis hispanica* and *P. peloponnesiaca*, the relative length of the hindlimbs is retained in males but falls substantially in females. *Lacerta bedriagae*, *L. laevis*, *L. danfordi* and *L. perspicillata* appear to show some decline in relative rate of limb growth in both sexes, perhaps after a slight initial rise, but the decline is more marked in females. In cases where relative limb length changes with body size, it is important to compare males and females of similar head and body length when assessing sexual differences in limb proportions.

Evolutionary plasticity of limb proportions

It will be seen from Table 1 that hindlimb span often varies substantially among closely related species, for instance within the genus *Mesalina* and within the *Lacerta agilis* group (*L. agilis*, *L. trilineata*, *L. viridis* etc.). This is also sometimes true of forms successively derived from a lineage, such as the genera of the Armatured clade. Such variation suggests that hind limb proportions relative to the body length are quite plastic in evolutionary time, something cor-

roborated by the varying amount of sexual dimorphism and the very different growth patterns encountered. Lineage effects (Arnold, 1994b) in the form of phylogenetic, and specifically developmental, constraint, consequently do not seem to be important in restricting change in relative hind-limb length.

Although there is a clear tendency among species and sexes for increase in relative hind-limb length to be associated with increased difference between fore and hindlimbs, this is also unlikely to represent a strong developmental constraint as the scatter of points in Fig. 3 around the general trend is very substantial. Forms like *Poromera* and *Psammodromus algirus* have similar relative hind limb lengths but differ substantially in forelimb/hindlimb ratios. Conversely *Latastia longicaudata* and *Meroles anchietae* possess a similar forelimb/hindlimb ratio but differ greatly in relative hind limb length. Again, although differences between sexes often follow the general trend between species, there are cases where this is not so.

It is noteworthy that the primitive Palaearctic assemblage and more primitive members of the Armatured clade have quite short legs but, given the general plasticity of limb proportions, this seems unlikely to represent a developmental constraint and may simply reflect the habitats they usually occupy. The limb proportions of *Psammodromus algirus*, which belongs to the primitive Palaearctic assemblage but often runs on the ground in open areas, as well as climbing, approach those of advanced armatured forms that are nearly all found in such situations.

Functional aspects of differences in limb proportions

Given the plasticity of limb proportions in lacertid lizards and their correlation with kinds of habitats occupied, it would not be surprising if differences between species reflected the functional problems of locomotion in particular environments and were produced by natural selection. A more detailed case for this is given in the rest of this paper but likely advantages of different limb proportions are briefly summarised here. Ground dwelling forms from open habitats get most of their forward thrust when running from the hind limbs. Such thrust is enhanced by greater general hind-limb length relative to the forelimbs, and an extended crus reflected in increased tibial length relative to the femur. The openness of the habitat allows such long hind limbs to be used effectively and probable increase in mass of the caudifemoralis longus muscle increases the power of what is a high-gear system of locomotion that delivers the high speeds necessary to evade predators in situations where cover is sparse.

In contrast, ground dwelling forms that spend considerable time in dense vegetation benefit from generally short limbs which can be deployed in the restricted spaces available. Speeds are lower but concealment from predators is easier. Possibly the greater relative length of the forelimbs reflects greater use in locomotion. Thrust from the small hindlimbs may not be optimal for locomotion and the flexibility of an often relatively long body may reduce its effective transmission. In these circumstances some traction by the forelimbs may be advantageous.

Climbers in vegetation matrixes have similar proportions to those just discussed and are likely to encounter similar locomotory problems. Another factor favouring short limbs in climbers in general is that they give low gearing which is likely to be beneficial when moving upwards against the force of gravity. The relatively long forelimbs in these forms may also allow them to contribute effectively to upward locomotion and they are also important in securing the foreparts, which are above the centre of gravity of the lizard as a whole during vertical climbing and so liable to fall away from the surface being climbed if unattached.

Differences in the caudifemoralis longus muscle

The caudifemoralis longus is the main muscle retracting the femur in lizards and runs from the femoral trochanter posteriorly on to the proximal caudal vertebrae to which it attaches by multiple heads (see e.g. Russell & Bauer, 1992; Arnold, 1994a). The muscle is roughly triangular in shape and its tapering posterior section extends backwards to caudal vertebra 6–13 in lacertids, usually reaching beyond the first autotomy plane discernable in radiographs. The number of autotomic vertebrae to which the caudifemoralis attaches ranges from one to six (L. Hartley, E. N. Arnold, pers. obs). The fact that the muscle extends beyond the first autotomy plane means that some of the most posterior part of the muscle may be lost as a result of caudal autotomy if breakage occurs far proximally, a not uncommon event in some species, for instance *Lacerta vivipara* (Barbadillo *et al.*, 1995). However the effect of such loss on limb function may be relatively small, for the bulk of the muscle lies anterior to the first autotomy plane and the fact that there are attachments to a number of nonautotomic vertebrae means that loss of the posterior section will not result in general loss of function.

There is a phylogenetic regularity in the position of the first caudal autotomy plane discernible in radiographs. In more basal lacertids this is usually on the fourth to seventh caudal vertebra but in most *Nucras* and in its advanced sister group there is a posterior shift and the first plane is usually no further forwards than the eighth vertebra. This shift may mean that the bulk of the caudifemoralis longus is

increased in these lizards and the proportion that remains after proximal autotomy is certainly larger. The number of non-autotomic vertebrae tends to be higher in males than females which means the former may possess a greater bulk of muscle to retract their relatively longer hind legs.

General anatomy of the hind leg (Fig. 5)

In advanced ground dwellers of the Armatured clade, the more distal elements of the hind limb are elongated and it is possible for the leg to be extended until it is more or less straight. The knee is essentially a ginglymus, that is a hinge joint moving mainly in a single plane, but does not run perpendicular to the long axis of the femur instead being angled mesially (Rewcastle, 1980). This results in a complex flexure of the crus on the femur in three dimensions. The mesotarsal joint between the crus and the metatarsal segment of the limb which runs between the astragalo-calcaneum and the other tibial bones, is also primarily a hinge joint and the foot can be extended in line with the crus or flexed until it is more or less parallel with it. However, these hinge joints in the hind leg do not have movement entirely confined to one direction. The crus can twist or swing to a small extent relative to the femur and the foot can flex inwards relative to the crus, some additional motion taking place at the base of the metatarsals. The foot can also twist on the crus to some extent. The hind limb of climbing lizards like *Lacerta oxycephala* is similar, but the distal segments are less elongated and the foot is usually inflected mesially.

Structure of the pes

In this and following descriptions feet are assumed to be placed sole-down on a horizontal surface. The lacertid pes exhibits essentially the primitive lizard structure with no loss or increase of elements in the tarsus, metatarsus or phalanges, the phalangeal formula being 2,3,4,5,4. Digits articulate with the metatarsals via ball and cup joints that allow considerable movement in all directions; in contrast the joints between the distal claw-bearing phalanges and the penultimate ones are double-headed ginglymi that are tightly bound and only permit the claw to move in the vertical plane.

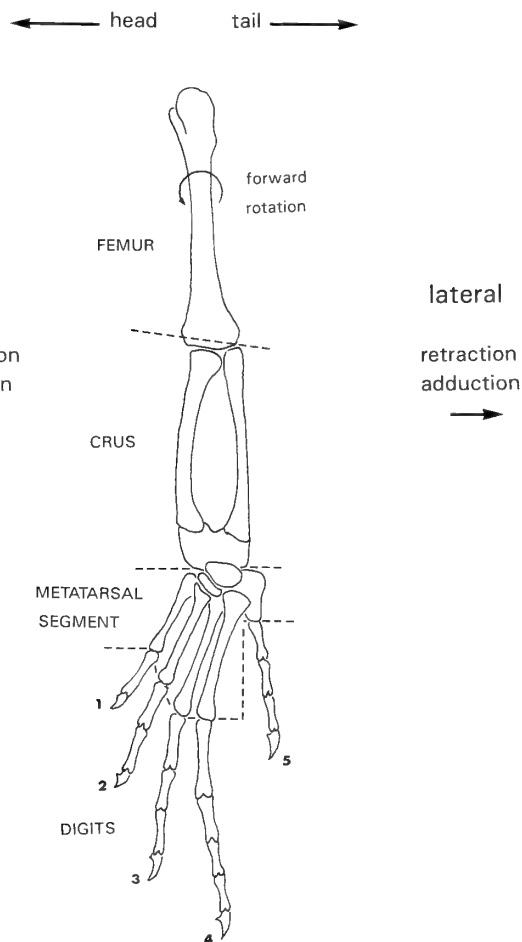


Fig. 5 Skeleton of left hind limb of lacertid from above, showing main elements and regions, orientation and directions of movement.

Table 2 Characteristics of the pes in ground dwelling and climbing lacertids (see Figs 7–10).

	Ground dwelling (e.g. <i>Acanthodactylus</i>)	Climbing (e.g. <i>L. oxycephala</i>)
Relative length of metatarsal bones	4 longer than 3	3 longer than 4
Digits 1–4	long	shorter
Relative length of metatarsal + digits 3 and 4	4 markedly longer than 3	4 not much longer than 3
Size of digit 5	short, often minaturised	long
Shape of digits 3–5 in lateral view	gently curved ventrally or straight	clearly kinked
Cross section of digits	rounded	latero-mesially compressed
Shape of phalanges	robust	more slender
Prepenultimate phalanx of digits 2–4 markedly shorter than contiguous ones	no	yes
Claw	long and shallow	short and deep
Articulations within digits	double-headed	simple
Mesial flexibility of digits 1–4	restricted	substantial

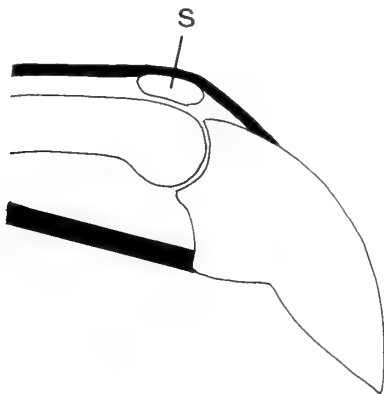


Fig. 6 Lateral view of the bones of the distal part of the digit of a climbing lacertid, showing dorsal and ventral tendons (black) attaching to deep, claw-bearing distal phalanx. The sesamoid bone (s), which can slide on the surface of the penultimate phalanx, displaces the dorsal tendon away from the hinge-line of the articulation between the two phalanges, increasing its moment arm around the centre of rotation and its efficacy in raising the distal phalanx and its claw.

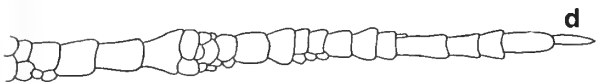
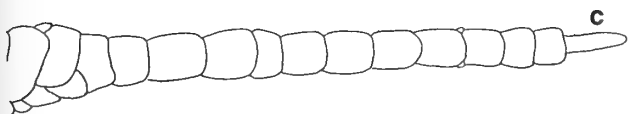
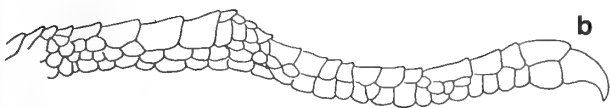
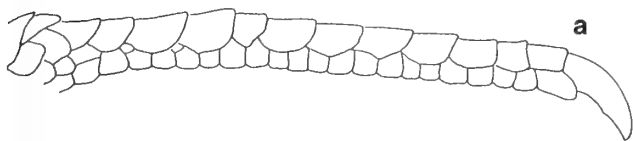


Fig. 7 Lateral and dorsal views of fourth hind digits. a., c. Ground-dwelling lacertid, *Lacerta agilis*. b., d. Specialised climber, *Lacerta oxycephala*.

The dorsal tendon of each digit which inserts on the final claw-bearing phalanx encloses a small sesamoid bone that lies close to the articulation of this phalanx with the penultimate one (Fig. 6). This digital sesamoid acts like a more familiar one, the patella (knee cap) of many mammals, in enhancing the efficacy of the tendon by moving it away from the hinge-line of the articulation and increasing its moment arm around the centre of rotation of the distal phalanx (Curry, 1984).

There are considerable differences in proportions of the pes and in shape and relative orientation of the phalanges and claws. The extremes are found in strictly ground dwelling forms, especially the more advanced members of the Armatured clade, and in those that climb extensively on steep open continuous surfaces. Basic differences are summarised in Table 2.

The pes in ground dwelling lacertids from open situations (Figs 7a,c, 8a, 9a, 10a).

In advanced members of the Armatured clade, like *Acanthodactylus*, the whole foot is large and metatarsal bones 1 to 4, and the digits arising from these, are especially long and increase successively in length. In some instances, such as *Heliobolus lugubris* the metatarsal bones are more or less parallel and bound closely together. Digits 1–4 are also elongated but digit 5, which arises from the highly modified fifth metatarsal bone, is frequently short and may be miniaturised, its phalanges and claw being much smaller than those of other toes. In extreme cases like *Heliobolus lugubris*, the whole fifth toe only extends as far as the distal end of metatarsal 4. Similar substantial reduction also occurs in *Ichnotropis capensis*. Toes are straight or gently curved ventrally when at rest (Fig. 9a) and are rounded in cross section (Fig. 10a). The phalanges themselves are robust (Fig. 9a) and tend to become steadily shorter distally in each digit. Although the prepenultimate phalanx of toes 3 and 4, may sometimes be a little shorter than contiguous ones this is not very marked. The terminal phalanx of each digit and the claw that covers it is relatively long, shallow and curves gently downwards. The prominence on the terminal phalanx, to which the ventral tendon of the digit is attached, is relatively close to the centre of rotation of the claw (Fig. 17c).

Articulations within the digits are double consisting of two horizontally arranged protruberences on the distal end of each phalanx that fit into two hollows on the proximal end of the adjoining one. Although the articulations all appear at first sight to be ginglymi, only the most distal one totally restricts movement to the vertical plane. The others in digits 2–4 allow these toes to be flexed laterally so they can curve quite easily in this direction, even though they are rather stiff basally. However, mesial flexion of these digits is more restricted and they can only form a gentle curve in this direction. The different extents of lateral and of mesial movement within these digits presumably depends on the degree of restriction produced by the ligamentous connections on each side of the articulations and by accessory tendons. Digit 5 swings easily around its base but joints within it, while allowing some movement, are generally stiffer in the horizontal plane than those in digits 2–4. All digits can be flexed extensively downwards and upwards when the muscles controlling them are relaxed.

Similar structure of the pes is found throughout the open-ground forms that constitute the clade made up of *Latastia* and its advanced sister group; it is also approached in many aspects in such ground-dwelling primitive Palaearctic species as *Lacerta agilis* (Fig. 9a, 10a).

The pes in lacertids regularly climbing on steep open surfaces (Figs 7b, d, 8b, 9b–e, 10b).

In *Lacerta oxycephala*, a species that habitually climbs on precipitous rock outcrops (Arnold, 1987), the foot is small and metatarsal

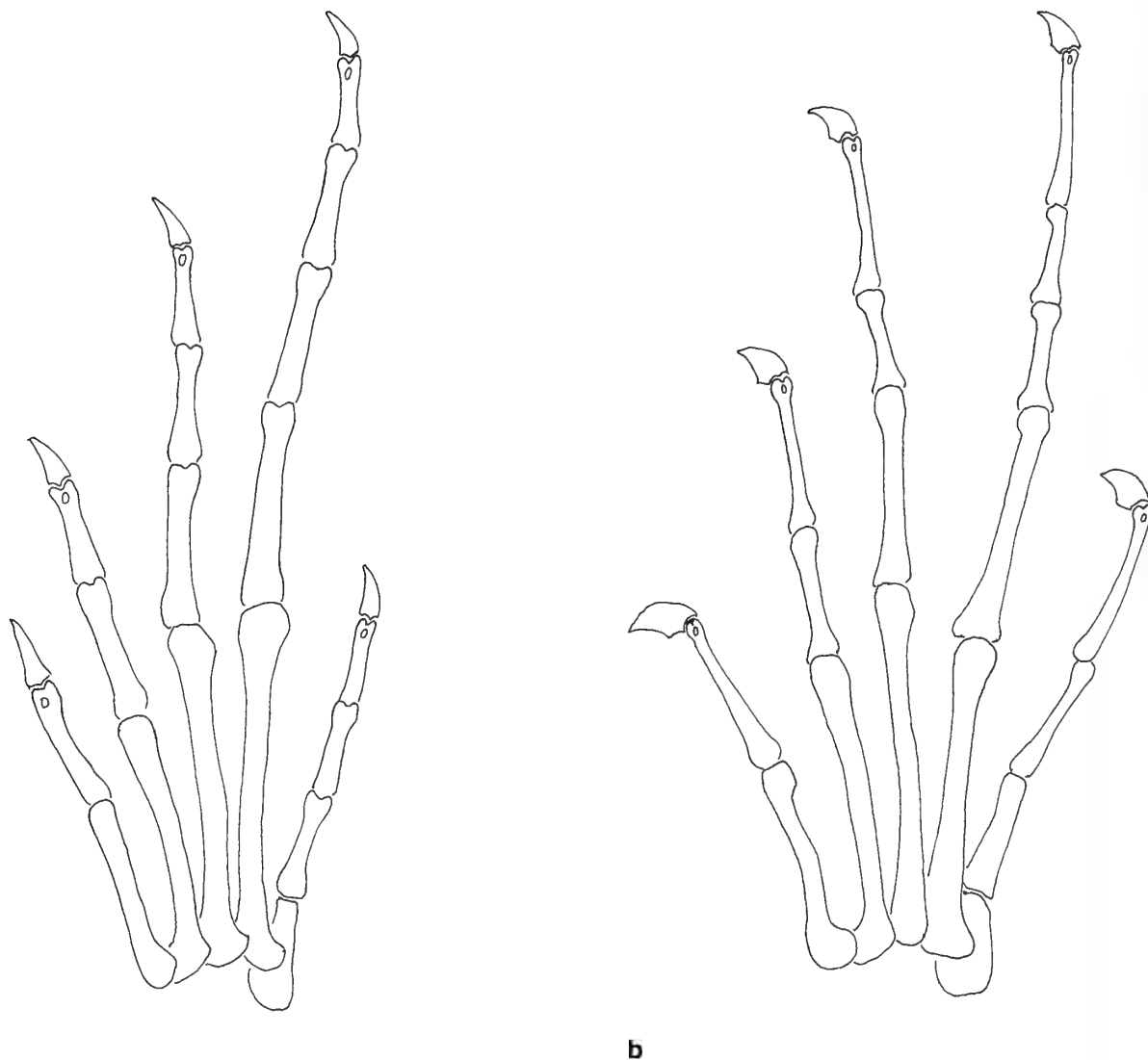


Fig. 8 Dorsal views of right pes of lacertids (digit 1 to left). a. Ground dwelling *Acanthodactylus erythrurus*: metatarsal 4 longest, digit articulations double headed, digit 5 miniaturised. b. Rock climbing *Lacerta oxycephala*: metatarsal 3 longest, digit articulations single, digit 5 large, phalanges slender, intermediate ones in digits 3 and 4 relatively short. For other differences, see Table 2.

bones 1–4, and the digits that arise from them, are quite short. The metatarsals and digits exhibit an increase in length from number 1 to 3 but metatarsal 4 is shorter than metatarsal 3 and, although digits 1–4 increase in length, the shortness of metatarsal 4 results in digit 4 projecting only a comparatively short distance beyond digit 3. Digit 5 is relatively long and unminiaturised, the articulation of its second and third phalanges being about level with the distal end of metatarsal 4. When at rest, digits 3–5 are distinctly kinked in the sagittal plane with abrupt changes of direction along their length (Fig. 9b–d). In digit 3, phalanx 2 is directed downwards, 3 upwards and 4 downwards. In digit 4, phalanx 2 is directed downwards, 3 approaches the horizontal, 4 is flexed upwards and 5 downwards. In digit 5, phalanx 2 is directed upwards, 3 is roughly horizontal and 4 flexed downwards, but there is sometimes marked deviation from this pattern (see p. 77). Kinking when digits are at rest appears to be maintained partly by the form of the envelope of skin that surrounds each digit and that of the ligamentous connexions that surround each interphalangeal joint. If the digit of a live lizard is stretched by

pulling the claw, kinking disappears temporarily, but it is transiently increased if the tension in the tendons lying dorsal and ventral to the phalanges is raised by the action of the muscles that activate them. Kinking is often especially marked in animals preserved in alcohol or formalin because shrinkage of muscle tissue produces similar tension in the tendons.

The digits are mesiolaterally compressed when transversely sectioned through a phalanx (Fig. 10b), instead of having a more rounded profile like ground dwellers. This difference results from the relative thicknesses of the phalanges and the surrounding tendons, especially the ventral ones. In ground dwellers the latter may be considerably more slender than the robust phalanges above them, while in climbers like *Lacerta oxycephala*, where the phalanges are more delicate in build, the stout ventral tendons may be as thick as thicker than these. The penultimate phalanx of each digit is long and gently curved downwards while phalanx 2 in digit 3 and phalanges 2 and 3 in digit 4 are shorter than those proximal and distal to them. The terminal phalanx of each digit and the claw that covers it is short,

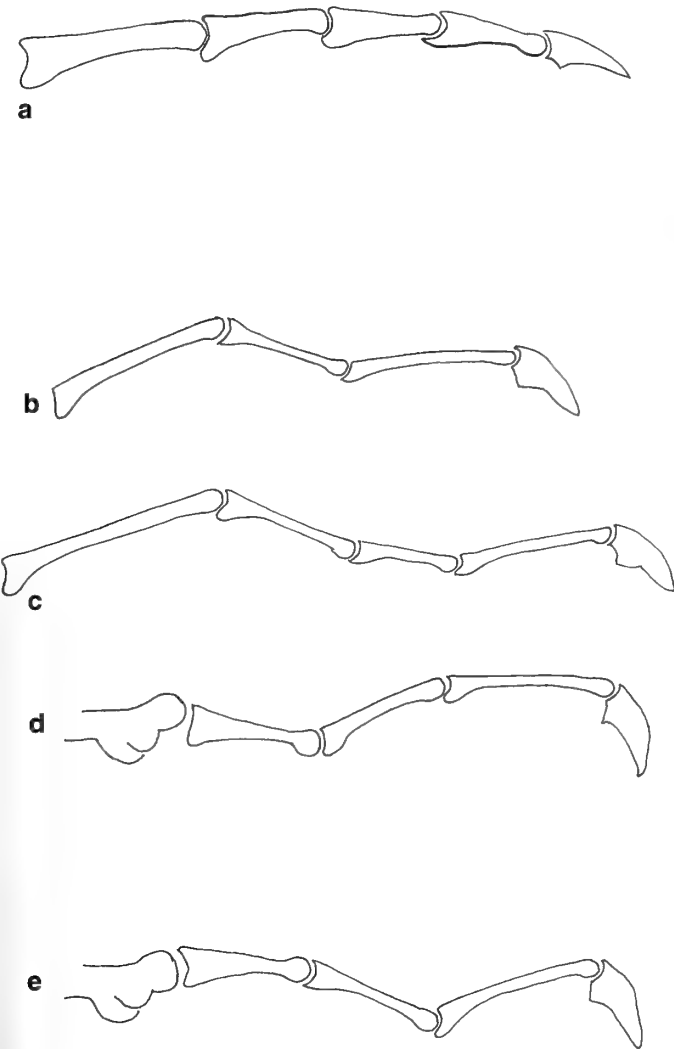


Fig. 9 Digits of pes of lacertids in lateral view. a. Ground dweller, *Lacerta agilis*, digit 4. b–d. Climbing species, *Lacerta oxycephala*, digits 3, 4 and 5. e. Climbing species, *Lacerta perspicillata* showing alternative pattern of flexion in digit 5.

deep and strongly recurved. The prominence on the terminal phalanx, to which the ventral tendon of the digit is attached, is situated well away from the centre of rotation of the claw, conferring considerable mechanical advantage (Fig. 17b). The tendon stands well away from the articulation when the claw is ventriflexted; it also tends to do the same under the downflexed joint between phalanges 1 and 2 in digits 3 and 4 (Fig. 17b), and 2 and 3 in digit 5.

Articulations within the digit except for the most distal one are simple, consisting of a single protruberance at the distal end of each phalanx that fits into a cup on the adjoining one. These confer substantial mobility in both the vertical and horizontal planes. As in ground dwellers, digits 2–4 can curve laterally and swing mesially around their base until their proximal phalanges are in line with their metatarsals. Unlike those of ground dwellers, the digits themselves can bend quite abruptly in a mesial direction, as a result especially of flexibility at their penultimate articulations but also, to some extent, of that at the articulations between phalanges 1 and 2 in digits 3 and 4 and that between 2 and 3 in digit 5. Toe 5 is not only lateromesially mobile at its base but also at other joints.

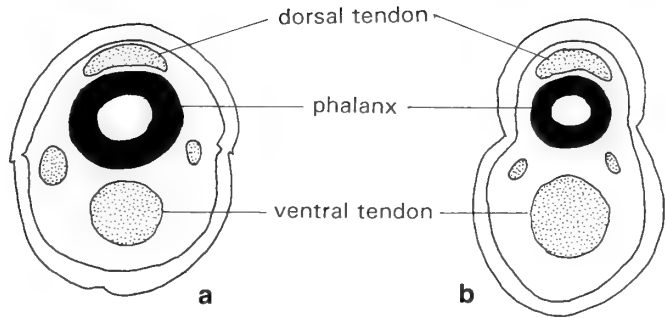


Fig. 10 Diagrammatic transverse sections of toe 4 of a. *Lacerta agilis* and b. *Lacerta oxycephala*, showing differences in relative cross sectional area of phalanx and ventral tendon.

Variations in the direction of kinking in toe 5 of lacertids

Most climbing lacertids possess a pattern of kinking in toe 5 like that found in *Lacerta oxycephala* and described above (Fig. 9d, called here pattern A). However, a minority possess a condition where phalanx 2 is directed downwards, 3 upwards and 4 downwards (Fig. 9e, called here pattern B). Pattern B is found in *Lacerta l. laevis*, *L. l. troodica*, many *L. kulzeri*, *L. chlorogaster*, *L. dugesii* and *L. perspicillata*, *Algyroides*, and the Equatorial African group (Fig. 2) of the Armatured clade; it occurs in weaker form in *Takydromus* and *Poromera*. This variant has consequently evolved perhaps seven times and, at least in Equatorial African group, in *L. chlorogaster* and probably elsewhere, seems likely to have had developed in ancestors that exhibited pattern A. In spite of pattern B originating on several occasions, the details of kinking in toe 5 are often stable across quite large and varied clades, for instance the Equatorial African group. Interestingly, many of the lacertid taxa showing pattern B are known to climb on vegetable structures, such as tree boles and flimsy herbage, which might at first sight suggest that it confers some performance advantage in these specialised situations (but see below)

Patterns of digital kinking in climbers of other families

Many other lizards that climb habitually have kinked digits on the pes and also often on the manus. Attention will be directed here to forms with simple toes, without the complex adhesive pads that occur in many geckoes and anoles. As in the digits of lacertids, the distal part of toes consists of an upwardly directed arc which may contain three phalanges (pattern A) or just two (pattern B).

These patterns occur in various combinations on digits 3, 4 and 5 of the pes and a particular combination for these three toes can be specified simply by a three letter code, for instance for lacertids this would be most usually B.B.A but sometimes B.B.B. There is also some variation in the orientation of the more proximal phalanges of toes 3–5 but this will not be discussed further here. Observed patterns in the distal parts of toes 3–5 in a range of lizards are given below.

A.A.A. *Petrosaurus mearnsi* (Phrynosomatidae); *Plica plica*# (Tropiduridae); *Gonocephalus modestus*#, *Draco blanfordii*# (Agamidae); *Agamura persica*, *Cyrtodactylus consobrinus*# (Gekkonidae); *Xantusia henshawi*, *Lepidophyma flavimaculata* (Xantusiidae); *Platysaurus*, *Pseudocordylus* (Cordylidae); *Mabuya quinquetaeniata* (Scincidae).

A.B.A *Tropidurus torquatus* (Tropiduridae).

B.B.A *Agama caudospinosa* (Agamidae), most lacertids.

B.B.B. *Varanus indicus*#, *V. mitchelli*#, *V. tristis*# (Varanidae); *Cryptoblepharus boutoni* (Scincidae); several lacertids#.

B.A.B. *Cnemaspis africanus* # (Gekkonidae).

When three toes are considered, there are eight possible combinations of the two patterns of kinking. BBB* (3), BBA* (2), BAB* (1), BAA, ABB, ABA* (1), AAB, AAA* (9). Five of these (asterisked) have already been observed in the small sample of climbing lizards examined; figures in parentheses indicate the number of cases encountered of each.

As already noted, pattern B in toe 5 is most usual among lacertids in forms that climb on vegetable structures (marked#), but when members of other families are also considered it is clear there are species with fifth toes exhibiting pattern A in this situation. Overall, there is no obvious correlation of pattern B with climbing on vegetable structures in any of toes 3–5.

The widespread occurrence of toe kinking in climbing lizards and its repeated evolution suggests that it confers performance advantage in this locomotory situation. However, the variety of patterns, including differences in the more proximal parts of toes 3–5, and the fact that they occur in various combinations in these toes, suggests that the exact arrangement of phalanges may be rather arbitrary in functional terms. Nonetheless, the existence of a particular pattern across some clades within the Lacertidae indicates that, once a pattern for a toe has become established, it may persist for long periods, even though multiple shift from pattern A to pattern B in toe 5 has also occurred. If the pattern of kinking is more or less arbitrary in functional terms, shift from one to the other might sometimes occur after an intervening non-climbing phase when the initial pattern was lost, but there is no overt evidence for such interludes.

The structure of the manus

As with the pes, the lacertid manus always possesses the primitive lizard phalangeal formula, which in this case is 2,3,4,5,3. The manus is also like the pes in the way the digits articulate with the metacarpals via ball and cup joints and in having terminal articulations that are tightly bound gynglymi with associated sesamoid bones. Metacarpal 3 is always the longest and numbers 1 and 5 the shortest, the digits are more equal in length than those of the pes and are capable of being broadly spread.

The manus in ground dwelling lacertids from open situations (Fig. 11a, Table 3)

In advanced members of the Armatured clade, the manus is often quite small compared with the pes although this differential is less obvious in species from soft-sand habitats. The longest digit is usually number 3 or this is subequal to 4. Toes are straight or gently curved ventrally and are rounded in cross section. The phalanges are often very robust, frequently more so than in the pes, and except for the terminal ones, tend to be subequal within a digit. The relative brevity of toe 4, which has most phalanges, means that these are particularly short. The final phalanx of each digit and the claw that covers it tends to be long, shallow and curves gently downwards. Articulations within digits are double and, as in the pes, mesial flexion of the toes is restricted.

The manus in lacertids regularly climbing on steep open surfaces (Figs 11b,c, Table 3)

In forms like *Lacerta oxycephala*, the manus is smaller than the pes but comparatively much larger than in many ground dwellers. The longest digit is usually number 4 and digits are lateromesially compressed; numbers 3 and 4 are flexed downwards at the articulation of phalanges 1 and 2, and somewhat upwards at the penultimate articulation, as in the other digits. Phalanges are slender, the penultimate ones being relatively long and slightly curved downwards; phalanx number 2 of digits 3 and 4 and also number 3 of the latter are

Table 3 Characteristics of the manus in ground dwelling and climbing lacertids (see Fig. 11). Differences in transverse section of the digits, shape of phalanges, claws and articulations within digits are similar to those in the pes.

	Ground (e.g. <i>Acanthodactylus</i>)	Climbing (<i>L. oxycephala</i>)
Longest digit	3, or 3 and 4 subequal	4
Phalange 2 of digits 3 and 4 and phalanx 3 of digit 4 shortened	weakly	strongly
Phalange 2 of toes 3 and 4 flexed downwards	no	yes
Digits can be very widely spread	no	yes
Mesial flexibility of digits	restricted	substantial

shorter than the ones bordering them. The final phalanx of each digit and the claw that covers it is short deep and recurved. As in the pes, the main ventral tendons are offset in the regions where digits are flexed downwards. Articulations within the digits are simple involving a single cup and ball arrangement and the digits can be abruptly flexed in the horizontal plane both mesially and laterally, especially in the area of the penultimate articulation.

The manus of *Holaspis guentheri* (Fig. 11c) deviates considerably from that characteristic of other lacertids climbing on continuous open surfaces. Digits 2–5 are more subequal in length, and numbers 3 and 4 are conjoined for the length of their first phalanx, penultimate phalanges are extremely long and more curved ventrally than in other lacertids and phalanx 2 of toe 3 and phalanges 2 and 3 of toe 4 are very short and flexed downwards. This degree of distinctiveness in the manus of *Holaspis* contrasts with that of the pes which, although it has the features usually associated with climbing on open surfaces better developed than in *Lacerta oxycephala*, does not differ radically from this species in its general form.

Characteristics of the feet in other lacertids

The numerous primitive Palaearctic lacertids and more basal members of the Armatured clade that climb to a significant extent on open surfaces have at least less marked versions of the foot characters that form a syndrome in a specialised climber like *L. oxycephala*, although the foot tends to be longer. Thus, the claws are relatively deep, the toes compressed and kinked, and metatarsal 3 is longer than 4 in the pes. These features occur, for instance, in many 'archaeolacertas', some *Podarcis* such as *P. hispanica*, *Algyroides nigropunctatus* and *A. marchi*, members of the *Lacerta agilis* group but not *L. agilis* itself, *Gallotia*, *Psammmodromus algirus*, *Australolacerta* and most members of the Equatorial African group. Independent shifts to the more marked version of the syndrome are found in such frequent climbers as *Lacerta perspicillata*, *Omanosaura* and especially *Holaspis*.

Forms that climb in vegetation matrixes, like *Gastropholis*, some *Takydromus* and *Poromera*, tend to have relatively weak versions of the climbing pattern but may also possess distinctive features for instance, in the latter two genera, separation between the digits may extend proximally between the distal parts of the metacarpals and metatarsals, allowing wider spread of the digits.

The manus and pes features that characterise advanced ground-dwelling members of the Armatured clade have developed in other ground-dwelling lacertids, at least in restricted form. Thus metatarsal 4 is about equal to number 3 in *Lacerta agilis*, *Psammmodromus hispanicus* and *Adolfus allenii* and is longer in some *Podarcis* that run extensively on the ground, such as *P. sicula* and *P. taurica*. Digit 5 of

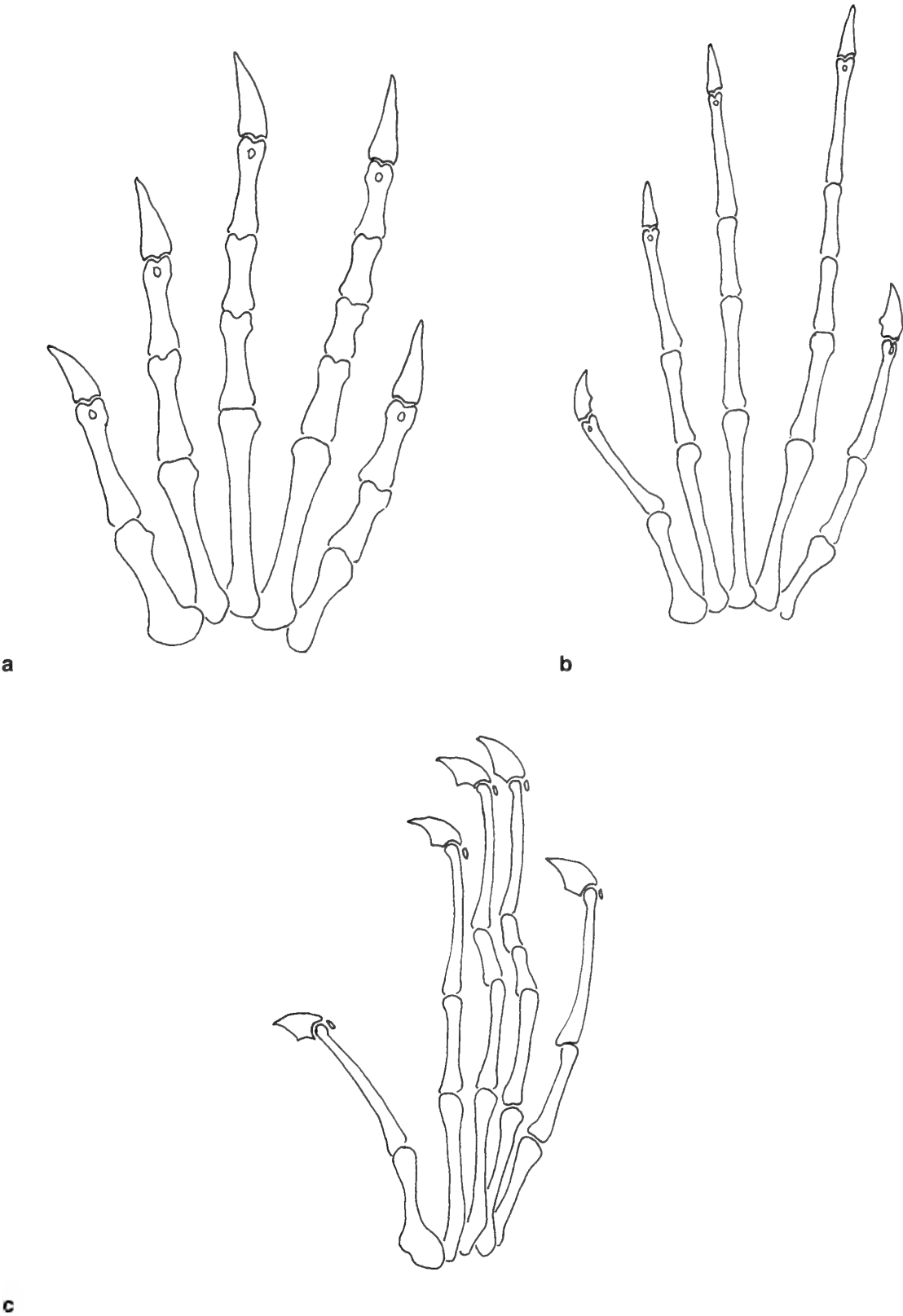


Fig. 11 Right manus of lacertids (digit 1 to left), a., b. dorsal, c. anterodorsal. a. Ground dwelling *Acanthodactylus erythrurus*: digit 3 longest, phalanges robust. b. Rock climbing *Lacerta oxycephala*: digit 4 longest, phalanges slender. c. *Holaspis guentheri*: toe 5 long, toes 3 and 4 strongly kinked. See Table 2 for other differences between a. and b.

the pes may be small in some of these forms and the digits are often not strongly kinked and have robust subequal phalanges and rounded cross sections. The syndrome is best developed as whole in *Psammodromus hispanicus* and *L. agilis*.

In some cases, a mixture of features typical of ground-dwelling and other activities occur. This may be a result of functional compromises, for instance in forms that are substantially ground dwelling but also occur in other situations. In *Lacerta vivipara*, a ground form that spends substantial time in dense grassy vegetation, many features associated with ground dwelling are present but metatarsal 4 is short and toe 5 quite long. Possibly the way the feet of this species are used in traversing vegetation has similarities to climbing. In *Poromera*, the foot has some features associated with ground locomotion and some with climbing quite strongly developed. However, in spite of probably sometimes climbing in vegetation, the hands and feet of *Philochortus* are essentially of the ground type.

Overall, direction of change in foot morphology appears to follow closely that of structural niche in lacertids (p. 00).

The variations in the pes found in lacertids are paralleled quite closely in some other families. For instance, within the sister group of lacertids, the Teiioidea, the Teiidae which are mainly ground dwelling in open situations have the pedal characteristics of lacertids occupying similar structural habitats. As here, the fifth toe is usually miniaturised and in *Teius* disappears entirely, something that also occurs in the ground running agamid *Sitana* (Russell and Rewcastle, 1979).

Special structures of the digits

In primitive Palaearctic lacertids and more basal members of the Armatured clade including *Nucras*, the toes are covered above with a single row of unkeeled scales along their length and below by a row of scales or lamellae that correspond more or less to those above. The lower row is often tubercular and each scale may be divided centrally, although this feature varies considerably, sometimes even among subdigital scales on the same toe. A number of modifications of this primitive external toe structure occur.

Expanded subdigital lamellae

Takydromus kuehnei is unique among lacertids in having the more proximal subdigital lamellae of the digits clearly expanded laterally to form a narrow pad superficially similar to those of geckoes such as *Cyrtodactylus*. This feature, towards which there is a slight tendency in some other *Takydromus*, may possibly enhance adhesion on the surfaces of the vegetation, among which these lizards are often found, by increasing the lower surface of the toes. However, SEM studies reveal no microornamentation of adhesive setae on the subdigital lamellae of *Takydromus kuehnei* (pers. obs.), such as are found in other pad bearing climbing forms including many geckoes and anoles, and the skink, *Prasinohaema virens* (Williams & Peterson, 1982).

Keeling of subdigital scales

Instead of being tubercular, the scales beneath the digits of lacertids may bear keels which, in ventral view, appear more or less parallel to the axis of the digit. In these cases the free edge of each scale and its keels are directed obliquely downwards, the latter ending in projections. When a toe is put down on a smooth flat surface, contact with this is largely limited to these points. Downwardly directed scales with keels ending in projections also occur on the palms and soles.

A tendency to keeling, often with considerable individual variation occurs in most *Psammodromus* species and in *Philochortus*.

Fully developed and consistent keeling is found in the advanced clade of ground dwellers in the Armatured clade that constitutes the sister group of *Philochortus*. Full keeling has evolved independently in *Psammodromus hispanicus* (presumably from the intermediate condition in other members of the genus), in *Omanosaura cyanura*, and in *Lacerta cappadocica*; there are thus four origins of the condition within the Lacertidae.

The number of keels on subdigital lamellae varies: two is most frequent but there are sometimes several, something which is commoner on the manus than the pes. Single keels also occur, in *Lacerta cappadocica* and in dune dwelling species of *Meroles*, *Acanthodactylus* and *Eremias* in which they are associated with less downward projection of the edge of the scale and little development of projections at the tips of the keels. In at least the first two genera, the shift to single keels has happened more than once.

Keeling on subdigital scales may vary within a species, for example there may be one to several in different populations of *Acanthodactylus grandis* (Arnold, 1983). This suggests keeling is quite labile in detailed form. Species that live exclusively on very fine aeolian sand may lose keeling secondarily, something that has developed independently in *Meroles anchietae* and *Eremias* (*Scapteira*).

Evolutionary shift to keeling does not appear to be related to changed locomotory requirements and instead may be more important in protecting the toes from high temperatures (Arnold, 1973). Some desert lacertids are at least briefly active on surfaces as hot as 60°C (pers. obs.), even though their digits incorporate delicate blood vessels and nerves. In this situation, limiting contact with the ground largely to the projections at the end of keels is likely to reduce heat intake, especially as keratin, of which the subdigital lamellae are formed, is a good insulator. If this is so, keeling may not be important as such but only as a means of providing support for the projections that actually contact the ground. Similar support of projections by keels is found in the belly scales of many *Takydromus* species, although here the projections appear more important in increasing frictional contact rather than in insulation (Arnold, 1997).

In the Armatured clade, the shift to keeling is associated with movement into hot open ground habitats and the same is true in *Psammodromus*. The *Lacerta* and *Omanosaura* with keeled digits are rock-dwellers but in particularly warm areas.

It is not clear why aeolian sand species often exhibit reduction from double or multiple to single keels with less downward inflexion of the free edges of the subdigital scales, and sometimes totally lose these features. One possibility is that the keeling and the associated projections will not be able to keep the digits substantially out of contact with the ground, because the toes of running lizards usually sink into soft sand, at least to some extent, so projections supported by keels will not restrict contact. In fact, the sinking may also reduce the problem of heat load since the digits are only briefly in contact with the very hot uppermost layer of sand and pass rapidly through it into the rather cooler layers below.

Outside the Lacertidae, digital keeling occurs in many other lizard families and is usually associated with hot substrata. It is found in many iguanians, scincids and cordylids that occur in sunny situations, but is absent in largely nocturnal or mesic clades such as gekkotans, xantusiids and anguids. The development of full keeling is probably associated with modest body size, a situation in which the problems of overheating of the extremities are likely to be particularly acute.

Digital fringes

Lateral and often mesial fringes of pointed scales on the digits have developed in at least five separate clades of the Lacertidae: in

Acanthodactylus, *Meroles*, *Eremias*, *Holaspis* and, in restricted form, in *Pseuderemias*. In *Acanthodactylus* a lateral scale row is present on the digits of manus and pes of all species, but an additional mesial row has developed on the manus perhaps three or more times in groups living mainly on soft sand (Arnold, 1983; Harris, Arnold & Thomas, submitted b). *Meroles* is similar in that all species have a lateral scale row on all digits, and a mesial row on those of the manus in a clade found on soft sand, consisting of the subgenus *Saurites* and *Meroles anchietae*. A mesial row occurs on the pes as well in *Meroles anchietae* which is found in the most extreme of such habitats (Arnold, 1991). Lateral and mesial scale rows have also evolved on all feet in the aeolian sand species of *Eremias* (*Scapteira*). *Holaspis* is distinctive in exhibiting additional scale rows only on some of the digits of the pes: digits 3 and 4 possess lateral and mesial rows, while digit 5 has a lateral row which is continuous with similar scales on the trailing edge of the hind leg and the sides of the tail.

In sand dwelling forms, the additional scale rows on the digits, which are often elongated and projecting, act rather like snow shoes during locomotion, reducing the tendency of the feet to sink into the yielding substratum (Carothers, 1986; Luke, 1986) and thus increasing effective thrust when running. However, it is notable that, although ground dwelling lizards obtain most locomotory thrust from the hind legs (p. 000), additional mesial rows of scales develop first on the manus. This may be because the forefeet especially are used in digging for food and to construct burrows and in this situation the fringes increase the efficacy of digging by broadening the toes so they shift more sand. Possibly, where sand is not especially soft, the functional advantage of an additional scale row is more critical in digging than running.

Although lateral expansion of the digits appears to confer advantage when running and digging in soft sand situations, it is less clear why expansion should be achieved by separate additional scale rows in lacertids, since some sand-dwelling lizards in other families merely have the usual dorsal and ventral scale rows on the digits extended horizontally to form fringes (Luke, 1986). Indeed in sand lacertids without a mesial row, the dorsal scale row may project in this way. Possibly, separate rows of scales on the sides of the digits do not actually give better function, in impeding the toes when they are pressed into the substratum, than fringes produced from dorsal and ventral rows. They may however be advantageous in environments where sand is very soft because fringes made up of independent scale rows can flex more easily ventrally, reducing impedance when digits are withdrawn from the sand.

In contrast to their function in sand dwellers, the additional digital scale rows of *Holaspis* probably provide extra lift when this unique lacertid glides through the air (Arnold, 1989b). In some iguanians such fringes permit the lizards to run across the surface of water (Luke, 1986). Although fringes made up of additional scale rows on the digits thus occur in three superficially quite different situations, in all of them they slow or prevent passage of the feet through fluids.

Not only have digital fringes in lacertids been elaborated by subsequent addition of separate lateral scale rows, but the length of the scales forming these also varies, often showing considerable correlation within a genus with the softness of the substratum usually occupied (Arnold, 1983). However, although some members of primarily sand dwelling clades appear to have reverted to firmer substrata, for instance *Meroles suborbitalis*, there are no certain cases where additional digital scale rows have been subsequently lost even though their degree of projection may be reduced.

LOCOMOTION AND FUNCTION

Some aspects of locomotion in habitual open ground lizards and in climbers are contrasted in Table 4

Locomotion in ground dwellers of the Armatured clade (Figs 12–13)

The following observations are based on *Heliobolus lugubris*, *Meroles cuneirostris*, *M. reticulatus*, *M. anchietae*, *Eremias arguta*, *Acanthodactylus boskianus* and *A. pardalis*. These were either videoed dorsally and laterally at 25 fields/sec and an exposure of 1/1000 sec., or filmed at 16–48 frames/sec. *Meroles cuneirostris* was also videoed at 200 fields/sec. Most runs were conducted on a flat cork surface but animals were also allowed to sprint across soft sand and the footprints produced used to check stride length and relative thrust of the fore and hind feet, as indicated by pressure waves in the sand produced at the trailing edge of the prints.

Lacertid lizards use all four legs when running. The gait is sprawling, that is the humeri and femora project from the body roughly in the horizontal plane, and the steps of individual limbs can be divided into two phases: the power stroke when the limb is retracted and actually delivers thrust, and the recovery stroke when it is brought rapidly forwards in preparation for the next step. Typically the fore and hind limbs work in diagonal pairs, for instance, the right foreleg and left hindleg are brought forwards in the recovery stroke at about the same time and are retracted more or less together in the power stroke; there may however be a slight lag, so that a hindlimb starts to move forwards after the contralateral forelimb.

At extreme phases of the locomotory cycle, the forelimb on one side of the body is directed backwards and the hindlimb forwards, so they approach each other or overlap, while on the other side of the body the limbs are directed diametrically away from each other. In general, strictly ground-dwelling lizards of the Armatured clade carry the body well away from the substratum when running. At the end of the power stroke of a hind limb, the lizard may be balanced on the toes of a single foot and this is followed by a gliding phase when the animal ‘floats’ forwards with all limbs off the ground.

Because of this floating phase, the total stride of each limb pair, that is distance between ground contact of left and right feet, may be substantially greater than the anatomical stride which is the distance between the feet of a limb pair when they are maximally spread forwards and backwards. As forelimb span is much less than hindlimb span in ground dwellers, the difference between total and anatomical strides is much greater for the forelimbs and they are both off the ground for much longer periods than the hindlimbs.

The posterior body flexes laterally to some extent during rapid locomotion towards the side on which the hindlimb is moving

Table 4 Some characteristics of open ground and climbing locomotion in lacertids specialised to these activities.

	Fast ground	Vertical
Body close to substratum	no	yes
Anatomical stride of forelimbs	short	long
Hind leg delay	some	more
Crus extended right forwards	yes	no
Hind step length/snout-vent distance	often >21	often < 1
Floating phase	yes	no
3 legs often in contact	not usually	yes
Toe 5 makes positive grip	no	often
Rise on toe tips at end of stride	yes	no

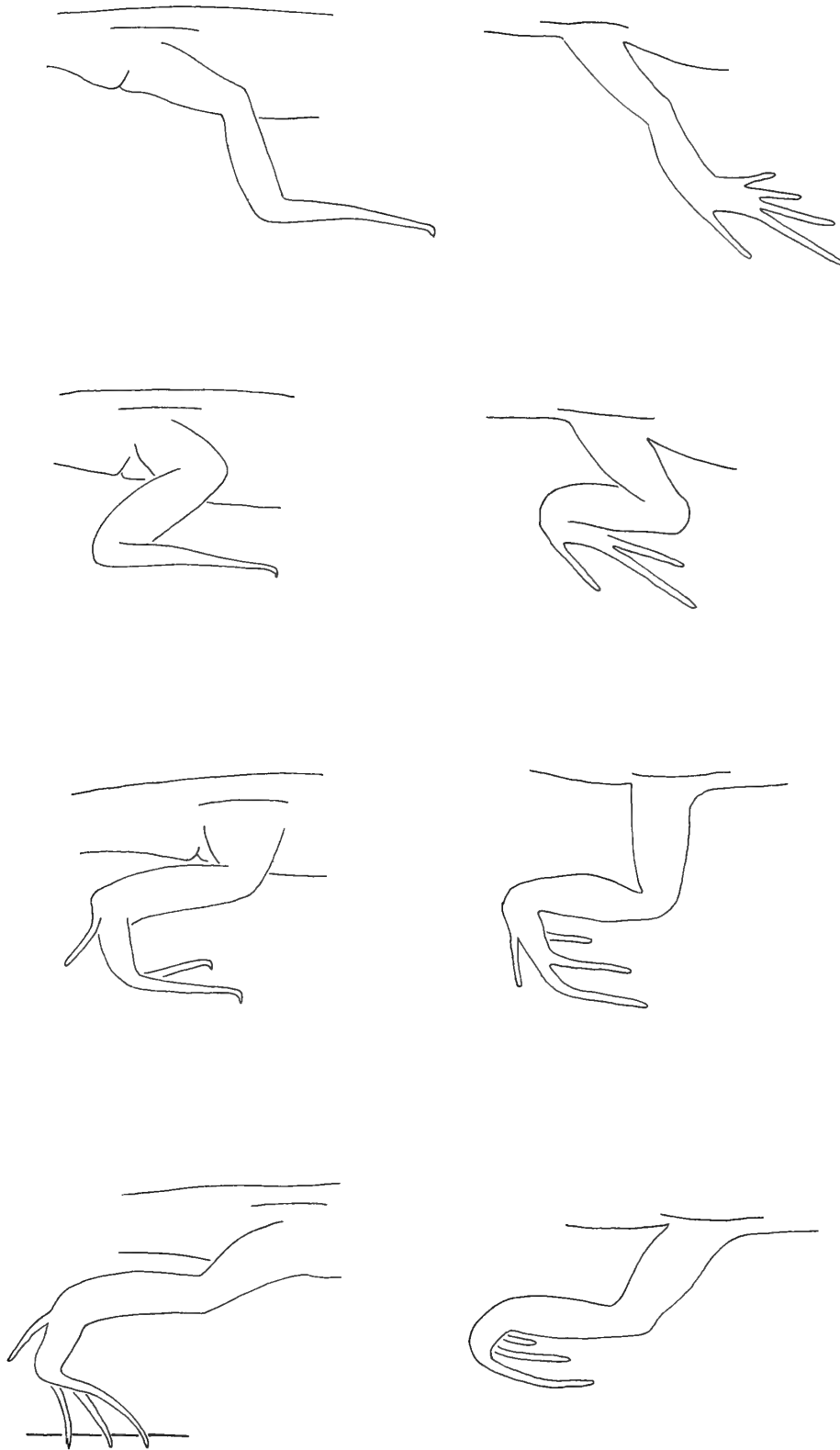


Fig. 12 Movements of hind leg of ground dwelling lacertid when running (left – lateral views, right – dorsal views). a. Beginning of power stroke: limb extended anterolaterally with toes 1–4 directed forwards and spread with claws inserted in substratum. b. Crus flexes on femur. c. Femur begins to retract, crus becomes more horizontal as femur rotates forwards and the metatarsal segment rises and is turned laterally bending the toes. d. Femur continues to retract, crus and metatarsal segment extends backwards and lizard rises on tips of toes 2–4.

forwards. This increases the length of the hind limb step which in the more long-legged species may be substantially longer than the body. Wild *Meroles anchietae* about 60mm from snout to vent had step lengths of 80–150mm (measured from tracks at Gobabeb, Central Namibia in April, 1994). As might be expected from the greater relative lengths of time they are in contact with the ground, hind limbs are far more important in fast ground locomotion than forelimbs. That they deliver more thrust can be seen from tracks in sand where hind limbs produce footprints with a strong posterior pressure wave caused by their powerful backward extension, whereas forelimbs tend to produce simple shallow pocks, indicating that their main role is to provide intermittent support to the foreparts.

Movements of the hind limb (Fig. 12)

When animals are running fast, the hind leg is brought forwards so that it is extended in generally anterolateral direction with the main axis of the metatarsal segment often lying approximately parasagittally or somewhat anterolaterally and digits 1–4 directed forwards and spread (Fig. 12a). The femur lies roughly in the horizontal plane, while the crus is directed obliquely downwards and the foot is placed flat on the ground with the claws of toes 1–4 flexed downwards and inserted into the substratum. Toe 5 often projects more laterally.

In the first phase of the power stroke, the crus flexes on the femur (Fig. 12b). This results in the femur moving forwards but, as the line of flexion of the knee is offset mesially, its distal extremity passes over the crus which changes orientation so that, from being directed anterolaterally, the crus swings until it is directed ventroposteriorly in a parasagittal plane.

At this stage, the femur begins to be retracted, its distal end descends somewhat and it also rotates forwards (when viewed from above) about its long axis (Fig. 12c). The crus also again becomes less flexed relative to the femur and these various movements change its orientation, so that it becomes more or less horizontal but still lies in a parasagittal plane. As this occurs, the metatarsal segment rises proximally, beginning with its lateral edge, so that it is now directed downwards and outwards. In firm substrata, the claws maintain their position so that this reorientation of the metatarsus then results in some mesial bending of the toes in the horizontal plane to accommodate it; however flexing is limited by the stiffness of the toes in this direction.

The femur continues to be retracted until it is directed anteroposteriorly (12d). At the same time the crus unflexes further so that it maintains its parasagittal orientation. By now, the metatarsal segment is completely lifted from the ground and this raises the base of the toes which, as well as being bent mesially, become flexed downwards and the lizard rises on to the tips of toes 1–4 and then just 2–4 so that, at this stage, it is hyperdigitigrade. Final thrust in the step is thus delivered entirely through the claws which act like the spikes on an athlete's running shoes. During this phase the whole leg extends and the upper surface of the metatarsal segment may even be directed anteroventally.

During a step, the lizard thus uses extension of all parts of the hindleg to provide thrust: femur, crus, metatarsals and digits. After this the muscles controlling the ventral tendons of toes 2–4 may relax so these digits dorsiflex and the claws are pulled free. Toe 5 plays very little part in fast locomotion in specialised ground dwellers and leaves the ground at an early stage.

In the rapid recovery stroke, where the hind limb is brought forwards before the next step, it is raised high, partly flexed and then extended forwards. During this process, the femur is protracted and its forward rotation is maintained, so that forward flexion and

extension of the leg takes place more or less in the horizontal plane and the foot is oriented with its mesial edge downwards. This allows the distal portions of the limb to be kept well clear of the ground, so that it is less likely to be impeded by any irregularities in the substratum or by projecting plants. It also means that when the foot does make contact with the substratum at the beginning of the power stroke, it may still be orientated with its mesial edge downwards, although it is then immediately placed flat on the ground as a result of backward rotation of the femur. If the toes do encounter an object that hinders their forward motion during the recovery stroke, the fact that the upper surface of the foot is directed forwards means that they can simply be passively ventriflexted and brushed aside, so the leg can still progress anteriorly. The toes are also capable of passive lateral movement around their joints with the metatarsals, especially when the foot is in the process of being placed sole-downwards on the ground.

There is some variation in fast hind leg motion in armatured ground-dwellers, which may partly result from the nature of the substratum and its irregularities. Thus the foot may be clearly directed anterolaterally at the beginning of the power stroke and the claws may slip in loose soils so that the foot tends to rotate outwards more at the end of a step. Some species also have characteristic features during fast ground locomotion; for instance, in *Acanthodactylus boskianus* the foreparts are carried particularly high.

Rotation of the femur and supposed restrictions on its movement

Rotation of the femur about its long axis is a very significant feature of hind leg movement during locomotion (Rewcastle, 1983). It enables the path of extension of the crus during the power stroke to be different from that of its flexion, allows the leg to be brought forwards orientated more or less in the horizontal plane well above the ground, and explains why the foot may be initially put down mesial edge first.

It has sometimes been assumed that the femur in lizards cannot be adducted far posteriorly because its trochanter was believed to jam against the ventral rim of the acetabulum (Rewcastle, 1983). However, in all the lacertids studied, substantial posterior adduction is regularly observed and no restriction of the kind envisaged is observable in skeletal material.

The supposed problem of crural rotation

There has been considerable discussion of a supposed problem of rotation within the distal hind limb (see for instance Rewcastle, 1983). If the foot is assumed to maintain its position during the power stroke, while the angle of the femur in the horizontal plane changes relative to it during adduction, there would have to be a rotational twist within the intervening crural area, to accommodate the change in relative position of these elements. The screw-like nature of the mesotarsal joint between the crus and foot actually permits some twisting (Rewcastle, 1980) and various other factors reduce the amount that is actually required: 1) The angle of the knee joint allows the crus to swing, from being in line with the femur at the beginning of the power stroke to being directed backwards, without disturbing the foot; 2) forward rotation of the femur and descent of its distal extremity also helps minimise twisting of the lower limb; this is also true of 3) reorientation of the metatarsal segment, 4) bending of the toes, and 5) the general mobility of the tarsal area. These factors, involving changes in orientation of the distal femur and of the proximal foot preclude any substantial problem of crural rotation.

A partial model of hind limb movement

The movements of the hind leg of lizards during locomotion take

place in three dimensions and are not always easy to envisage from a written description and diagrams. However a clearer idea of some of the main aspects can be obtained by making a simple model out of a strip of card with folds inserted to represent articulations between the main elements (Fig. 13). The model can be used to demonstrate the pattern of flexion between the femur and crus, the subsequent reorientation of the latter element in the parasagittal plane and associated lifting of the metatarsal segment brought about by partial retraction and rotation of the femur, the benefits of femoral rotation in allowing the limb to be partially retracted and extended in the horizontal plane as it is brought forwards in the recovery stroke, and the restricted nature of the problem of rotation in the crural region. It should however be born in mind that there is more play in the actual joints than the model indicates. Such a model is also useful in appreciating the rather different motions of the hind leg in climbing species.

Other hind limb gaits in ground-dwelling lizards – continuous gearing

Although lizards are often stated to have only a single gait, in contrast to many mammals, the hind limbs are used in a range of ways that are largely correlated with speed. Stationary lacertids may commence movement by thrusting with both hind legs, especially if startled, so accelerating before a step pattern is established. In slow walking, the excursion of the femur may be restricted and, instead of being brought forwards, the crus may be kept largely flexed, so that it is never directed forwards and the soles of the feet may be orientated rather laterally, a result of forward rotation of the femur.

At increasing speeds, femoral excursion is greater and the crus may be brought forwards until it is roughly perpendicular to the body with the foot directed anteroposteriorly. Finally, the crus is extended fully forwards and the femur rotated backwards at the beginning of the power stroke, as described above. These substantial changes in the way the hindlegs are used act like continuously variable gears. As might be expected, the body is held closer to the ground in the slower gaits as forward rotation of the femur during these permits a more lateral use of the whole limb.

Movements of the foreleg in ground-dwellers

At the beginning of the power stroke, the humerus is directed antero-laterally and the lower limb and digits point forwards. During retraction the forelimb turns over until its underside is uppermost. At first the manus is placed palm-down, but the lizard rises on the distal toes as the lower limb becomes more or less vertical. However, the toes usually dorsiflex at the end of the stride. As with the hind leg, the foreleg is raised high when it is brought forwards in the recovery stroke.

Functional aspects of the limbs and feet of ground-dwelling lacertids

It is now possible to assess the functional importance of limb morphology in ground dwelling lacertids. The long legs, in which the more distal elements – crus, metatarsal segment and digits – are differentially elongated, are responsible for the extended stride of these species, and the way the metatarsal bones are bound closely together in some forms increases the rigidity of the metatarsal

segment. The way the main adductor muscles, especially the caudifemoralis, are attached proximally to the femur confers high mechanical advantage on the locomotory system, which in this respect and the elongation of its distal elements parallels those of other fast amniote runners such as horses.

The regular downward curve of the toes, maintained by joint capsules and tension in the dorsal and especially ventral tendons at the end of the stride, and the restriction on medial flexion, ensure that thrust is delivered to the ground efficiently. The robust phalanges with joints of restricted flexibility are clearly suitable for resisting the compressive and shearing forces produced at this time, when the lizard may sometimes be balanced on the tips of very few toes. Steady increase in length from the first toe and its metatarsal to the fourth means that the claws of these digits can be well-spaced when inserted in the ground, ensuring a wide area of contact with the substratum so a good grip is more likely, even on shifting surfaces; the generally large size of the foot also contributes to this spread and the long lightly curved claws are more likely to gain effective purchase in earth or sand than short recurved ones. Reduction of the fifth toe is comprehensible in as much as it is virtually unused in fast locomotion.

The very robust phalanges of the manus may not be specifically associated with locomotion but could be important in digging, something advanced ground lacertids accomplish largely (or entirely in the case of *Heliobolus lugubris*, personal observations) with their forelegs. Possibly the relatively large manus of soft-sand dwellers is also functionally associated with digging.

Ground locomotion in climbing species

Lizards that habitually climb, like *Lacerta oxycephala*, *L. perspicillata* and to a lesser extent, *L. nairensis*, run quite efficiently on the ground and often extend the crus fully forwards. However, they tend to carry the body less high than specialised ground-dwellers, partly because their limbs are generally shorter and the crus especially so, and these features also limit stride length. Habitual climbers do not rise on to the tips of their toes at the end of the stride and, instead of the digits flexing downwards, they flex dorsally, toes 2–4 bending at the penultimate articulation between the phalanges, so the pes rotates over the inserted claws (Fig. 17b). This shortens effective stride length still further. Climbing species also tend to keep the hind limb closer to the substratum during the recovery stroke.

The distinctive features of ground locomotion in habitually climbing forms all have functional advantages during climbing (p. 000). A similar but more extensive carry over of features advantageous in climbing to horizontal locomotion occurs in the gecko, *Gekko gekko* (Zaaf, Aerts *et al.*, 1997).

Locomotion in climbers on steep open surfaces (Figs 13–17)

Most detailed observations were made of *Lacerta oxycephala*, which was filmed dorsally and laterally when climbing on a near vertical rock slab. *L. perspicillata*, *Algyroides nigropunctatus* and *A. marchi* were also examined by film or video; in most cases, speeds and exposures were the same as for many ground dwelling lizards but *Algyroides nigropunctatus* was also videoed at 200 fields/sec.

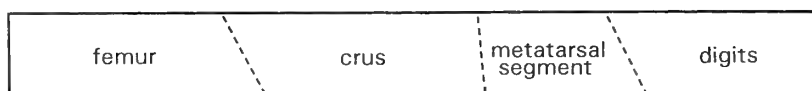


Fig. 13 Simple model of right hind limb of lacertid. A strip of card cut and folded as indicated by broken lines can be used to demonstrate the main movements of the hind leg elements in a running lizard.

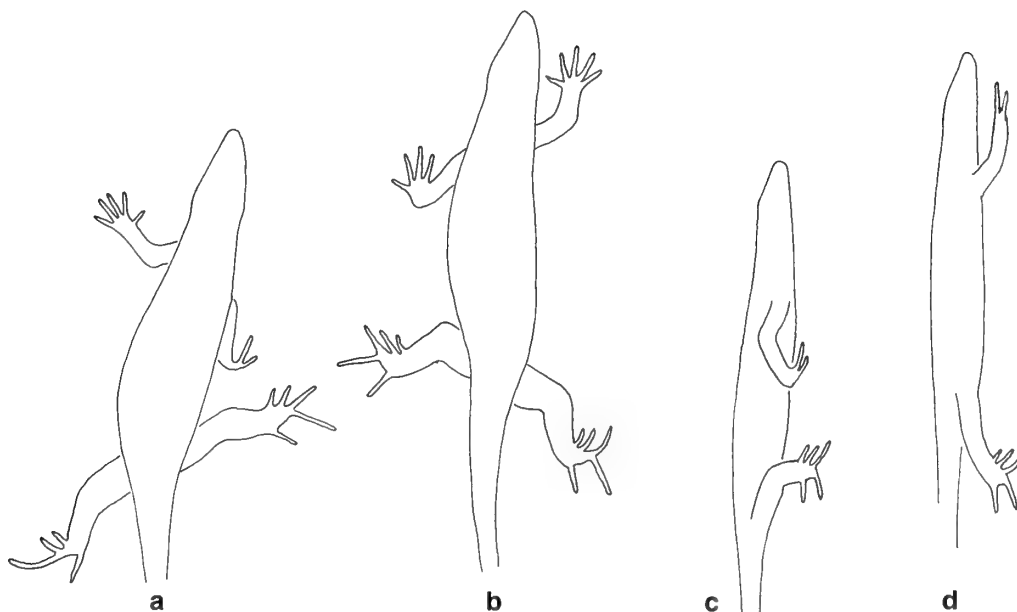


Fig. 14 Views of specialised climbing lacertid ascending vertical surface; a, b dorsal; c, d lateral. Crus and foot are not extended far forwards and hind digits flex mesially at end of power stroke, the body is kept very close to the surface being climbed.

Many lacertids climb on open continuous surfaces such as rocks and tree boles and branches. These vary in steepness, from gentle slopes to vertical and even overhanging surfaces, and lizards may run directly up them, or descend, or travel laterally or obliquely. Locomotion in specialised lacertid climbers often has many similarities to that of ground dwellers, but there are marked differences, especially when ascending perpendicular and near-vertical faces.

In this situation, a lizard like *Lacerta oxycephala* climbs with its body very close to the surface and the limbs spread laterally so the distal extremity of the femur does not pass dorsal to the crus during the power stroke (Fig. 14). As in ground dwellers, the limbs work in diagonal pairs. Each hind foot is placed lateral and posterior to the ipsilateral forefoot and the hind leg in each diagonal limb pair is delayed relative to the foreleg so that, as the recovery phase is brief, the proportion of time when two feet are out of contact with the substratum is small. In observed sequences of climbing in *Lacerta oxycephala*, the recovery phase took between an eighth and a quarter as long as the power phase, the smaller proportion being during slow

climbing. Counts of the number of frames of cine film in which four, three and two feet gripped the rock suggest that four legs may be in contact for over half, and three legs for over three-quarters of the total time; there is consequently no floating phase. This pattern contrasts strongly with fast locomotion in specialised ground dwellers where two legs are usually out of contact with the substratum and sometimes all four. The distance between the consecutive foot holds is more or less equal for both fore and hind limbs, being about half to three-quarters of the snout-vent distance in the locomotory sequences studied.

Movements of the hind limb

The excursion of the hind limbs is relatively restricted and although the femur is directed anterolaterally at the beginning of the power stroke (right hind limb, Fig. 14a,c), the crus is not brought fully forwards at this time and is usually, directed approximately normal to the body axis. The metatarsal segment, which is mesially inflected, is then directed anterolaterally and is placed flat on the substratum.

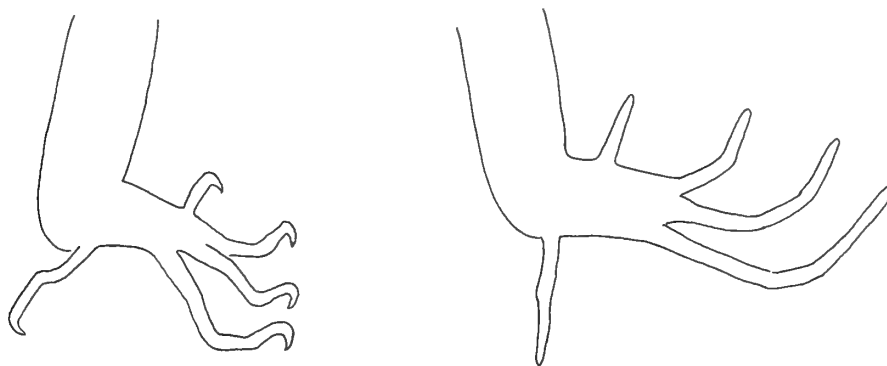


Fig. 15 Flexing in the hind toes of a climbing *Lacerta oxycephala* at the end of the step. a, oblique lateral view showing flexion in the sagittal plane of the toes. b, dorsal view, showing mesial flexion of toes 1-4.

Often the digits are spread radially with all the claws inserted in minor irregularities in the substratum and the well developed toe 5 contributing positively to the grip of the hind foot. Toes 1–3 are often directed more or less anteriorly, 4 laterally or somewhat posteriorly and 5 posteriorly. Sometimes, instead, toes 3 and 4 may both be directed obliquely backwards, or toes 1–4 are all directed forwards.

As the crus flexes on the femur and the body of the lizard moves forward, it becomes directed posterolaterally, changing its orientation to the foot. This results in the metatarsal segment being directed more laterally and its posterior edge rising; because the claws are firmly inserted, digits 1–4 flex mesially to accommodate this change in orientation of the metatarsal segment (right hind leg, Fig. 14b; Fig. 15). There is also a tendency for the crus to thrust diagonally backwards at this stage which accentuates the bending of the toes. At the same time, the proximal parts of toes 1–4 flex upwards in the vertical plane mainly at the following phalangeal articulations toe 1 – 0/1, toe 2 – 1/2, toe 3 – 2/3, toe 4 – 2/3 and 3/4.

The femur is then retracted and the crus is extended posteriorly relative to it, thrusting the body of the lizard upwards (right hind leg, Fig. 14b). The metatarsal segment does not rise much as a whole but its hind edge continues to do so and, as this happens, the claw of toe 5 becomes detached, followed by that of toe 4 (if this digit is not directed forwards), and then those of the remaining toes as the foot moves rapidly forwards to gain a new grip further up the rock face. This recovery stroke takes place with the foot close to the substratum.

In contrast to ground locomotion, the femur of specialised climbers seems to be rotated forwards around its long axis for most of the step cycle, allowing the limb to work largely in a plane more or less parallel to that of the substratum.

Movements of the fore limb

After its recovery stroke, the forelimb is extended forwards with the humerus directed roughly anterolaterally, the lower limb forwards and the digits broadly spread (right limb, Fig. 14b,d). As the humerus retracts and the lower limb flexes on it, the latter rotates in a parasagittal plane, becoming orientated first normal to the substratum and then directed posteroventrally as the limb thrusts backwards (right limb, Fig. 14a, c). After this the digits flex dorsally and the claws are then released from their contact with the rock face, as the next recovery stroke begins.

Other patterns of locomotion in specialised climbing lacertids

On less steep surfaces a climbing lizard like *Lacerta oxycephala* shifts to a locomotory pattern essentially similar to that which specialist climbers use on the ground (p. 85). When running down a very steep slope, upward motion is presumably powered substantially by gravity, but descent is controlled by the lizard taking short steps in which the hindlimbs are turned back with toes 4 and 5 and often 3 directed posteriorly (Fig. 16). At the end of a step, in which the femur is not moved much, the ventral tendons of these digits are relaxed, loosening the grip of the claws. The foot is then brought forwards, still directed posteriorly, and the claws flexed and inserted again; after this the leg extends backwards and the cycle is repeated.

Problems of upward vertical locomotion

The problems encountered by a lizard climbing a vertical face are quite different from those of an animal running on relatively level ground. 1. There is a need to keep upward thrust parallel with the surface being climbed. Although the oblique thrust delivered to the

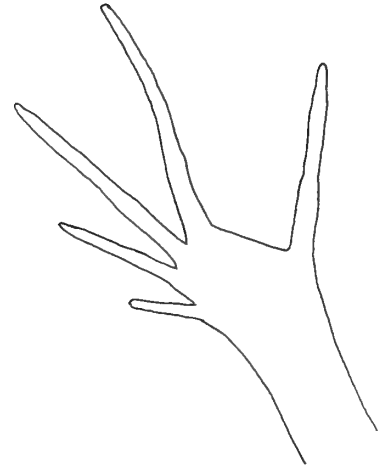


Fig. 16 Position of toes of right hind foot in *Lacerta oxycephala* descending a rock face; 3, 4 and 5 are turned posteriorly.

substratum by the hind limbs of a running lizard tends to push it a way from the ground into a floating phase, gravity returns it rapidly. There is no such automatic restoration of contact on a vertical face and oblique thrust would push the lizard right off the substratum. Thrust must consequently be applied in a direction parallel to the face. 2. There is a constant danger of falling from the face being climbed. In particular, were there no foreleg contact, a lizard would tend to fall outwards because it is then in a position of unstable equilibrium with its centre of gravity above the remaining hindleg contact. The converse condition, with both hind legs free, is less precarious as the posterior part of the body tends to rotate towards the rock. 3. As gravity acts in a direction diametrically opposite to that of locomotion, momentum will be lost very quickly once upward thrust ceases; this must therefore be regular and continuous.

Many characteristics of locomotion, in lacertids that climb vertical faces regularly, appear to ameliorate these problems. Keeping the body and limbs close and parallel to the surface being climbed ensures that backward thrust delivered through the claws is also more or less parallel to it. The danger of falling off the face is minimised by the way the number of feet in contact with it is maximised including those of the particularly important forelegs. This positive engagement of all feet in upward locomotion maximises thrust and makes it available throughout the cycle. Thrust is also maximised by the way flexion of the toes enables the claws to be kept in place as long as possible. Bringing the crus forwards until it is not much more than normal to the body axis is equivalent to moving in a relatively low gear, compared with the anterolateral extension found in ground runners travelling at speed, something that is also appropriate when moving against gravity. Keeping the body and limbs close to the substratum also maximises stride and restricts the downward leverage that the body would exert if it was held away from the substratum. The tail also plays a part in ensuring the foreparts of the lizard do not fall away from the face. It is held very close to the substratum and, if the front legs cannot get a grip (for instance if a piece of smooth card is interposed), the lizard can hold its upright position by stiffening its body and tail and pressing the latter against the surface.

Functional aspects of the limbs and feet of specialised climbing lacertids

The greater equality of fore and hind limb pairs in habitual climbers, when compared with open ground dwellers, is important in allowing the stride lengths of the two pairs to be matched and for the fore feet

to play a positive role in upward locomotion, presumably contributing thrust as well as attaching the foreparts. This contrasts with ground runners where the forelimbs have at most a minor role in delivering thrust. The fact that the hind limbs of habitual climbers are relatively short overall is partly responsible for the low gear nature of upward locomotion, as is the shortness of the crus compared with the femur; when the crus is flexed towards the substratum at some phases of the step cycle, its shortness permits the upper limbs and body to remain close to the substratum.

The short sharp recurved claws on the feet of climbing forms allow a firm grip on substrata like rock that do not permit much penetration. The insertion of the ventral tendon on the distal phalanx of each digit well away from the actual articulation (Fig. 17a, b) means that it has high mechanical advantage and can flex the claw effectively against the weight of the body, ensuring its grip is maintained.

At the end of the recovery stroke, when the hind foot is reattached to the substratum, the long third metatarsal allows the third toe to be deployed easily forwards, laterally or backwards, depending on where its claw can be inserted. The mobility of this toe and of numbers 4 and 5 means that some or all of them can be opposed to the remaining toes to give a positive grip on the substrate. The fact that toe 3 can be turned backwards is also important in allowing its claw to join those of digits 4 and 5 in acting as an intermittent brake when the lizard runs rapidly down steep slopes. When the digits of the hind foot are spread with their claws flexed and in the process of insertion in the rock face, the dorsal and ventral digital tendons contract emphasising the kinking of the phalanges in toes 3–5 and so shortening these digits. This shortening ensures a positive grip by the opposed claws.

Shortness of the hind toes in specialist climbers helps to reduce lateral foot displacement produced by outward thrust of the crus. In the later stages of the power stroke, mesial flexibility of toes 2–4 permits the claws to remain in place. As the metatarsal segment turns more laterally, these toes often become quite sharply bent in a plane parallel to the substratum. This permits the claws to remain in place and upward thrust to be generated for as long as possible. As the back of the metatarsal segment lifts, downward flexion of the second phalanges of toes 3 and especially 4 (Fig. 15a) enable the claws of these often backwardly or outwardly directed digits to remain in place longer, prolonging a positive grip.

Not only do forwardly directed toes flex mesially but, as the metatarsal segment lifts and turns over, hind toes 3 and 4 bend dorsally in the parasagittal plane if they are directed forwards (Fig. 17b). This flexion is concentrated at particular joints which enables it to be more acute than if it were distributed throughout most of the articulations of the toe; the shortness of some intermediate phalanges also contributes to this. Such acute flexion means that the metatarsal segment can stop closer to the rock face instead of being displaced outwards.

Concentration of dorsal flexion is combined with the simultaneous ventral flexion of the claw, necessary to maintain its grip and, in toes 3 and 4 and when backwardly directed, additional ventral flexion of phalanx 2 on phalanx 1. The areas of ventral flexion are produced by tension in the main ventral tendon. Although tension is likely to be more or less the same throughout the length of the tendon, ventriflexion is combined with the intervening area of the toe flexing dorsally. This differential action is an additional result of toe kinking, coupled with the varied positioning of the tendon relative to different articulations in the toe (Fig. 17a, b). Essentially under the joints where the more distal phalanges flex downwards, for instance in toe 4 at the articulation of phalanges 1 and 2 and 4 and 5, the tendon is displaced away from the joint. This differential

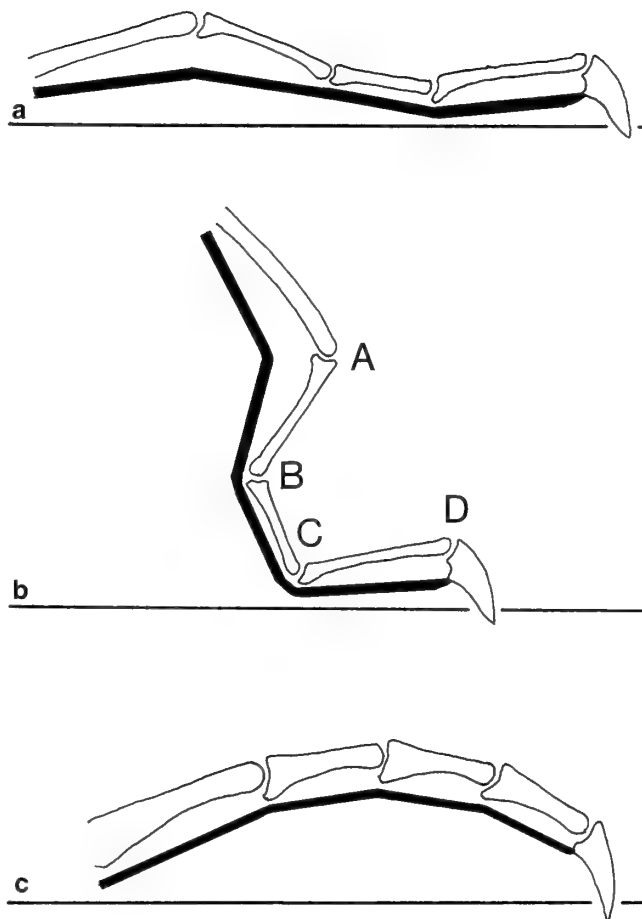


Fig. 17 Effects of digit kinking and tendon position. a. Fourth hind toe of *Lacerta oxycephala* with claw newly inserted in rock face. b. Same toe towards end of stride when metatarsal segment is lifting. Because the ventral tendon (black) is displaced well away from joints A and D and consequently has greater mechanical advantage at them, the articulations can be kept ventriflexed while joints B and C, where the tendon is closer and mechanical advantage less, can simultaneously dorsiflex in response to the movement of the metatarsal segment. Claw grip can consequently be maintained right to the end of the stride. c. Fourth hind toe of *Lacerta agilis*; because there is no inbuilt kinking or marked differential tendon displacement, the toe simply bows upwards when the ventral tendon is under tension

positioning means that the mechanical advantage of the tendon varies with the particular articulation to which it is applying a turning moment; thus advantage is great at the two articulations where it is displaced downwards but weaker in between where, in toe 4, phalanx 2 articulates with phalanx 3 and 3 with 4. Consequently the latter area can flex dorsally in response to lifting and forward movement of the metatarsal segment, while those bordering it retain their ventral flexion, maintaining the lowering of the toe below the level of the metatarsal segment and the grip of the claw. The way the toes of habitual climbers can flex simultaneously in two directions in a plane perpendicular to the substratum and also bend mesially contrasts with the situation in specialised ground dwellers. In these, because joints are double headed and because there is no kinking and the main ventral tendons do not show variation in degree of separation from particular joints, the digits simply curve upwards into a regular arc (Fig. 17c); this places substantial restrictions on the possibility of vertical climbing in these forms (see below).

Kinking of the hind toes of climbing lizards then is a very simple feature that has profound effects on foot function: toes 3–5 can be shortened to provide a positive grip; when directed backwards or outwards, they can be displaced downwards so that they maintain their claw contact with the substratum, even though the posterior part of the metatarsal segment to which they are attached is rising; simultaneous flexing in different directions in the parasagittal plane is possible. Not surprisingly, such a simple but elegant and productive mechanism has arisen many times in climbing lizards (see p. 77). As noted, it seems probable that the numerous variants in the exact pattern of kinking within the foot that are found in lizards as a whole (p. 77) are to a large extent functional alternatives rather than adaptations to different situations.

The forefoot shows some functional similarities to the hind one. The digits are spread very widely when the claws are first inserted and possibly contraction within the palm draws the metacarpals closer, tensioning the fingers. As in the hind limb, the shortness of intermediate phalanges in digits 3 and 4 probably concentrate dorsal flexion allowing it to be sharper and letting the forelimb be turned over without being displaced much outwards. The peculiarities in *Holaspis* have not been investigated in a living animal but they may allow the limb to act even more effectively in a parasagittal plane.

In general the digits of climbing lacertids act differently from those of habitual ground dwellers. Instead of the weight of the animal being balanced on columns of phalanges at times, it is supported by tension in the ventral tendons. The phalanges are subjected to a compressive force by this but, because the tendons are firmly attached by ligamentous sheaths at each joint, such force is along the length of the phalanx and consequently exerts little shear. Also, as the tendon insertion on the claw is offset from the pivot for this on the penultimate phalanx, thus increasing its mechanical advantage, compressive forces along the axes of the toes will be reduced. The largely tensile role of the toes in climbers is reflected in their slender phalanges and robust ventral tendons and the net lateromedial compression of the toe this produces compared with the toes of ground dwellers (Figs. 9b, 10).

Climbing in specialised ground dwelling lacertids

Members of the ground dwelling clade consisting of *Latastia* and its sister group are incompetent climbers. In trials using single lizards of each species, *Meroles reticulatus* could not climb a concrete slab that was at a much steeper than 60° from the horizontal; the maximum angle for *Acanthodactylus erythrurus* and *A. scutellatus* was 70°, and for *A. boskianus* 80°. In these species and other ground dwellers such as *Lacerta agilis*, the hind toes cannot flex mesially or dorsiflect as they do in specialised climbers; as already noted they simply bow upwards instead. In contrast, specialised climbers like *Lacerta oxycephala* and *L. perspicillata* could climb the slab with ease when it was vertical or even overhanging by 10° or 20°.

CONCLUDING REMARKS

Limb proportions and foot morphology of lacertid lizards are obviously evolutionarily plastic and numerous changes in these features have taken place within the family, often in different directions. However, although extreme variants are quite different, virtually no anatomical changes are obviously likely to be irreversible, in the way that loss of phalanges or claws that occur in many gekkotans seem to be. (Development of extra rows of scales on the sides of the toes may be a possible exception).

Across the family, changes in limb proportions and foot structure correlate quite closely with shifts in structural niche and the different

locomotory problems that these entail. It is possible to interpret the different morphologies in functional terms as conferring performance advantage in these situations. Clearly, locomotion in different habitats requires different morphological features, in particular, running on open ground, climbing on open surfaces and traversing vegetation matrixes. Adaptation to any one of these reduces locomotory effectiveness in the others. For instance, the robust, stiff digits that allow ground dwellers to run partly on their toe tips restrict climbing ability, while the flexible toes advantageous to climbers are inappropriate for the most effective kind of ground locomotion. Species which occur in a range of structural habitats consequently must compromise in locomotory terms and are probably not maximally effective in any one situation. Whether they always converge on a functionally intermediate morphology or whether it is sometimes more effective to be efficient in one area but accept penalties in another is not yet clear. However, *Podarcis peloponnesiaca* at Stymphalea, S. Greece, runs effectively on the ground and also climbs readily on rock outcrops but it is very clumsy in the latter situation compared with rock specialists. (Arnold, 1987).

The conflicting mechanical demands of locomotion in different environmental situations and the fact that they are largely unresolvable is one of the main reasons why mechanical aspects of habitat comprise such an important parameter in the structure of lizard communities (Arnold, 1984, 1987). Actually, it is not habitat *per se* that causes the conflict but the fact that really efficient physical compromises seem impossible.

Overall there is great homoplasy among lacertids not only in structural niche but also in the locomotory mechanisms associated with these.

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- Submitted, c. A phylogeny of the European lizard genus *Algyroides* Bibron & Bory 1833 (Reptilia: Lacertidae) based on DNA sequence, with comments on the evolution of the group.
- Submitted, d. Relationships and evolution of Wall lizards, *Podarcis* (Reptilia: Lacertidae) based on the partial mitochondrial DNA sequences.
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Heteroleotris georgegilli, a new species of gobiid fish, with notes on other Mauritian *Heteroleotris* species

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SYNOPSIS. *Heteroleotris georgegilli*, described from six specimens, 19.7–22.5 mm SL, is distinguished from congeners by the following combination of characters: second dorsal-fin rays I, 10–11, usually I, 10; anal-fin rays I, 9; scales ctenoid, restricted to posterior part of body and caudal peduncle (behind segmented dorsal-fin ray 5–7); and head pores present (posterior nasal, median anterior interorbital, posterior interorbital, infraorbital, postorbital and terminal lateral canal pores). Four additional *Heteroleotris* species are recorded from Mauritius: *H. apora*, *H. poecila*, *H. vinsoni* and *H. zanzibarensis*. The first-named two species represent new records for Mauritius. Limited data suggest that Mauritian *Heteroleotris* assort into different habitats.

INTRODUCTION

In 1995 the author participated in a six-week expedition to survey shorefishes of Mauritius, Indian Ocean, along with associates from the Smithsonian Institution, J.L.B. Smith Institute of Ichthyology and Port Elizabeth Museum. Among the fishes collected were six specimens of a new species of the genus *Heteroleotris* Bleeker, 1874. The new species is herein described and compared with congeners; other Mauritian *Heteroleotris* species are also discussed.

Heteroleotris species are distinguished from other gobiids by the following combination of characters: half or more of lower part of first gill slit closed by membrane; distinct, single-lobed mental frenum; distinctive superficial neuromast arrangement below eye (see Figs 1,2); first dorsal fin with six spines and pterygiophore formula of 3–22110; and vertebrae 10 + 17 (Akihito & Meguro, 1981; Hoese, 1986).

The genus is most diverse in the western Indian Ocean, with 13 species (revised by Hoese, 1986); the present study brings the total to 14. Only one described species [*H. poecila* (Fowler)] is known from the Pacific Ocean, but it also occurs in the Western Indian Ocean. However, Hoese (1986) noted that three undescribed species occur in the Pacific (one from the West Pacific, one from Rapa and one from Easter Island), and Gill & Reader (1992) recorded an additional undescribed species from Middleton and Elizabeth reefs, southern Coral Sea.

MATERIALS AND METHODS

Measurements to the snout tip were made to the midanterior tip of the upper jaw; standard length (SL) from the snout tip to the midposterior part of the hypural plate; head length from the snout tip to the posterior (vertical), fleshy edge of the operculum. Eye diameter was measured horizontally where greatest. Preanal, predorsal and prepelvic lengths were measured from the snout tip to the anterior edge of the first spine base of the relevant fin.

Distance between first and second dorsal-fin origins was measured between the anterior edges of the first spine base of each fin. Caudal peduncle depth was the shallowest depth of the peduncle. Caudal peduncle length was measured from the posterior edge of the last anal-fin ray base to the ventral edge of the caudal peduncle at the vertical through the posterior edge of the hypural plate. Fin ray lengths were measured from the bases of the rays to their tips. Caudal fin length was the length of the lowermost ray articulating with the upper hypural plate (*i.e.*, hypurals 3 + 4). Pectoral fin length was the length of the longest ray. Pelvic fin length was measured from the base of the spine to the distal tip of the fourth segmented ray. The pattern of interdigitation of first dorsal-fin pterygiophores with neural spines is given as a first dorsal pterygiophore formula following the methods of Birdsong *et al.* (1988). Terminology of head pores and other methods of counting and measuring follow Hoese (1986) or are self explanatory. Osteological details were determined from radiographs and from a paratype that was cleared and stained for cartilage and bone (Potthoff, 1984). Meristic and morphometric values are given first for the holotype, followed where different by value ranges or frequency distributions for the paratypes. Frequency distributions are presented in the form 'x fy,' where 'x' is the count and 'f' indicates that the following value, 'y,' is its frequency. Where counts were recorded bilaterally from the holotype, both values are presented and separated by a slash; the first value given is the left count.

Comparisons of *H. georgegilli* with congeners were based on published data (particularly those provided by Akihito & Meguro, 1981, and Hoese, 1986), specimens obtained in Mauritius by the author and colleagues (see below; museum codes follow Leviton *et al.*, 1985), and the following specimens in The Natural History Museum: *H. bipunctata* Tortonese, 1976, Yemen, Aden, BMNH 1985.7.29.3–6 (3); *H. diademata* (Rüppell, 1830), Gulf of Suez, BMNH 1925.12.31.51 (1; holotype of *Liotes* (*Pseudoliotes*) *simulans* Smith, 1958); *H. vulgare* (Klunzinger, 1871), Red Sea, BMNH 1979.6.20.40–43 (4); *H. zonata* (Fowler, 1934), South Africa, Durban, BMNH 1919.4.1.21–22 (2), Persian Gulf, BMNH 1900.5.8.93 (2), Mekran Coast, BMNH 1899.5.8.93 (1).

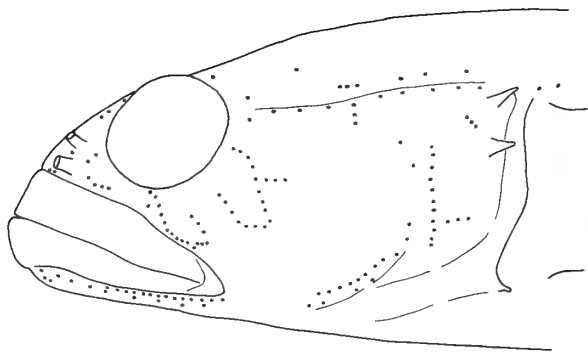


Fig. 1 *Heteroleotris apora*, diagram of head in lateral view showing positions of superficial neuromasts of laterosensory system (composite based on several specimens from Mauritius).

SYSTEMATIC ACCOUNT

Heteroleotris georgiegilli sp. nov.

Figs 2–6

HOLOTYPE. USNM 344315, 19.7 mm SL female, Mauritius, Flic en Flac, 30 m north of entrance to lagoon, 20°16'S 057°22'E, around small coral bommie on coral, coral-rock, sand and silt bottom, 4–10 m, A.C. Gill, D.G. Smith, M.J. Smale, W. Holleman, P. Clark and B. Galil, 05 May 1995 (field no. PCH 95-M20).

PARATYPES. Mauritius: BMNH 1997.10.24.1, 1: 20.3 mm SL female (subsequently cleared and stained), BMNH 1997.10.24.2, 1: 22.5 mm SL male, RUSI 56870, 1: 19.8 mm SL female, collected with holotype; USNM 344316, 1: 20.7 mm SL male, Albion, off Pointe Petite Riviere at end of Avenue Victory, surge area and adjacent gutters with sand, pebble and rock bottoms, 0–5 m, A.C. Gill, M.J. Smale and W. Holleman, 15 May 1995 (field no. PCH 95-M23); USNM 344317, 1: 22.3 mm SL male, Passe de L'Ambulante, off Le Morne, outside lagoon, 20°26'10"S 057°17'40"E, spur and groove with surge, 6–8 m, P.C. Heemstra, A.C. Gill, D.G. Smith,

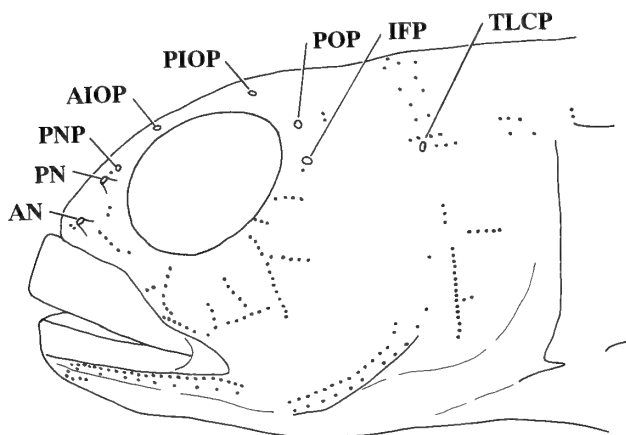


Fig. 2 *Heteroleotris georgiegilli*, diagram of head in lateral view showing positions of laterosensory pores and superficial neuromasts (composite, based primarily on holotype, USNM 344315, and cleared and stained paratype, BMNH 1997.10.24.1). Abbreviations: AIOP, anterior interorbital pore; AN, anterior nostril; IFP, infraorbital pore; PIO, posterior interorbital pore; PN, posterior nostril; PNP, posterior nasal pore; POP, postorbital pore; TLCP, terminal lateral canal pore.

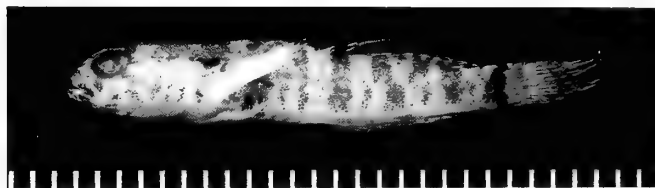


Fig. 3 *Heteroleotris georgiegilli*, holotype, USNM 344315, 19.7 mm SL, Flic en Flac, Mauritius.

M.J. Smale, W. Holleman, P. Clark, *et al.*, 18 May 1995 (field no. PCH 95-M30).

DIAGNOSIS. *Heteroleotris georgiegilli* is distinguished from congeners by the following combination of characters: second dorsal-fin rays I, 10–11, usually I, 10; anal-fin rays I, 9; scales ctenoid, restricted to posterior part of body and caudal peduncle (behind segmented dorsal-fin ray 5–7); and head pores present (posterior nasal, median anterior interorbital, posterior interorbital, infraorbital, postorbital and terminal lateral canal pores).

DESCRIPTION. Dorsal-fin rays VI + I, 10 (I, 10 f4; I, 11 f1); anal-fin rays I, 9; pectoral-fin pointed with 18/18 (16 f1; 17 f2; 18 f7) rays, the lower 1 (0 f8; 1 f2) ray unbranched, remaining rays branched; upper 3–5 pectoral-fin rays with free tips; lower pectoral-fin rays slightly thickened, more robust than upper rays; pelvic-fin rays I, 5; branches on first segmented pelvic-fin ray 5/4 (4 f10); branches on second pelvic-fin ray 5/5 (4 f4; 5 f5; 6 f1); branches on third pelvic-fin rays 6/6 (4 f1; 5 f6; 6 f3); branches on fourth segmented pelvic-fin ray 5/5 (3 f3; 4 f4; 5 f3); fifth 'segmented' pelvic-fin ray unbranched, with few or no segments, much shorter than other segmented rays (subequal to or shorter than spine) and inconspicuous (clearly visible only after dissection; Fig. 4); pelvic fins fully separate, without connecting membrane or fraenum (Fig. 5); segmented caudal-fin rays 9 + 8; branched caudal-fin rays 8 + 8 (7 + 7 f1; 8 + 7 f4); upper unsegmented caudal-fin rays 5 (4 f1; 5 f4); lower unsegmented caudal-fin rays 4 (4 f2; 5 f3); vertebrae 10 + 17; first dorsal pterygiophore formula 3-22110; anal pterygiophores preceding first haemal spine 2; epurals 1.

Scales ctenoid, restricted to posterior part of body and caudal peduncle, extending anteriorly as narrow midlateral wedge or band to vertical through second dorsal-fin segmented ray 6/5 (5 f5; 6 f4; 7 f1; Fig. 6); lateral scale rows 11/11 (10 f2; 11 f5; 12 f1; 13 f2).

First gill arch broadly joined to suspensorium by membrane; gill opening restricted to pectoral-fin base; branchiostegal rays 5.

Premaxilla with 3 or 4 irregular rows of conical teeth anteriorly,

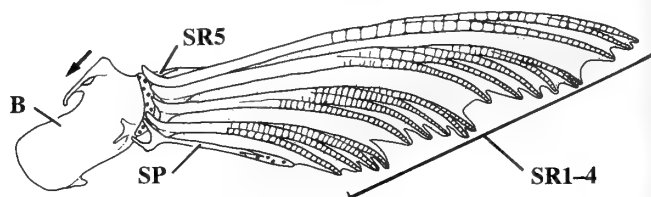


Fig. 4 *Heteroleotris georgiegilli*, cleared-and-stained paratype, BMNH 1997.10.24.1, 20.3 mm SL, ventral view of right pelvic fin and basipterygium. Abbreviations: B, basipterygium; SP, spine; SR 1–5, segmented rays 1–5. Large stipple indicates blue-stained material (see text); small stipple indicates interradi membranes. Arrow points anteriorly. Scale = 1 mm.

reducing to 1 or 2 rows posteriorly, the teeth of outer row largest and caniniform; inner row of teeth across front of premaxilla slightly curved and enlarged; dentary with 3 or 4 irregular rows of conical teeth anteriorly, reducing to a single row posteriorly, the outer row of teeth largest and caniniform; inner row of teeth across front of dentary slightly curved and enlarged; palatine and vomer edentate; tongue edentate and weakly rounded to truncate, sometimes with weak indentation anteriorly.

Cephalic sensory pores (see Fig. 2): posterior nasal 1/1; anterior interorbital 1; posterior interorbital 1; infraorbital 1/1; postorbital 1/1; lateral canal 0/0; terminal lateral canal 1/1. Distribution of superficial neuromasts (cutaneous papillae) on head as shown in Fig. 2. Male urogenital papilla pointed posteriorly, with inconspicuous lobe on either side of narrow gonopore, the posterior edge of papilla papillose; female urogenital papilla subrectangular, truncate, with weak lobe on each side of wide gonopore, the gonopore rim papillose. Epaxial musculature extending anteriorly to posterior interorbital pore.

As percentages of SL: head length 32.0 (30.7–32.4); eye diameter 9.6 (9.0–10.1); head width at posterior preopercular margin 24.9 (23.3–28.0); head depth at posterior preopercular margin 18.8 (17.5–19.7); body depth at pelvic-fin origin 20.3 (18.4–20.2); body depth at anal-fin origin 16.8 (16.2–17.2); caudal peduncle depth 11.2 (10.2–11.1); caudal peduncle length 19.3 (17.9–19.6); predorsal length 40.1 (38.1–39.4); prepelvic length 30.5 (28.9–31.3); preanal length 58.9 (58.6–60.0); distance between first and second dorsal-fin origins 19.3 (17.9–20.7); second dorsal-fin base length 27.4 (27.6–28.8); third dorsal-fin spine length 10.7 (11.6–14.3); third from last segmented dorsal-fin ray length 14.7 (14.5–16.1); anal-fin base length 23.9 (21.7–23.3); third from last segmented anal-fin ray length 14.7 (14.6–15.7); pectoral fin length 29.4 (27.1–30.5); pelvic fin length 22.8 (19.6–23.2); caudal fin length 24.9 (24.4–26.3).

COLOUR OF PRESERVED SPECIMENS. Head and body pale brown with dusky brown to grey-brown reticulate mottling, this darkest dorsally; mottling forming about eight weak bars, the first through upper base of pectoral fin, the last through base of caudal fin; last bar dark grey, distinctly darker than all other bars; dusky grey bar extending from anteroventral edge of eye to middle of upper lip, contiguous ventrally with dusky grey bar or spots on lower lip and

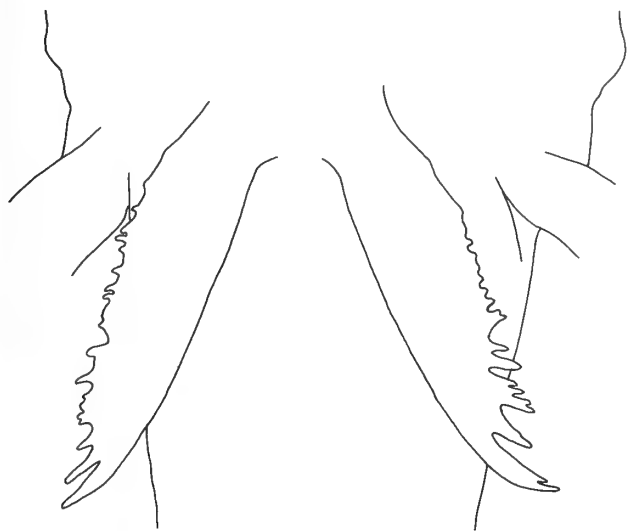


Fig. 5 *Hetereleotris georgegilli*, holotype, USNM 344315, 19.7 mm SL, outline of pelvic fins in ventral view.

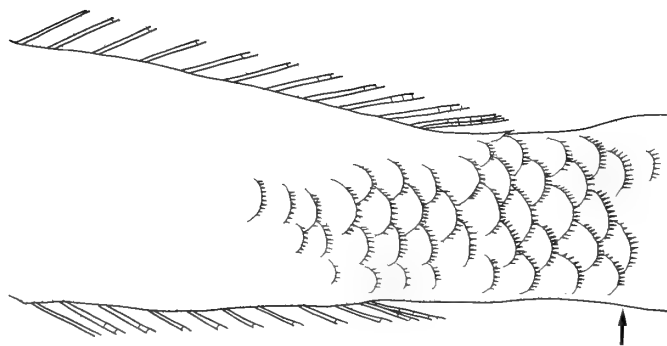


Fig. 6 *Hetereleotris georgegilli*, holotype, USNM 344315, 19.7 mm SL, diagram of posterior part of body and caudal peduncle showing scalation. Arrow indicates vertical through posterior edge of hypural plate.

chin; dark grey spot on upper part of pectoral-fin base, this extending on to basal third of upper few rays; dorsal fins pale to hyaline with diffuse dusky bars extending obliquely from each body bar; dorsal fin sometimes with dark grey distal margin (observed only in two of three males); anal fin pale to hyaline, sometimes with two or three irregular dusky grey stripes; caudal fin pale to hyaline, with dark grey basal bar (see above) and about five to eight irregular dusky bars; pectoral fins pale to hyaline with dark grey spot dorsally (see above) and irregular dusky bars; large white spot immediately below and behind dark spot on upper part of pectoral fin, the white spot edged posteriorly in dusky to dark grey; pelvic fins pale, sometimes with scattered melanophores basally.

COLOUR IN LIFE. Not recorded.

ETYMOLOGY. The specific epithet is in memory of my father, George Burton Gill (1925–1994).

COMPARISONS WITH OTHER *HETERELEOTRIS* SPECIES. Hoese's (1986) key to western Indian Ocean *Hetereleotris* identifies specimens of *H. georgegilli* as *H. nebulofasciata* (Smith, 1958), a species currently known only from east Africa (Kenya to Mozambique) and the Comores (R. Winterbottom, pers. comm.). *Hetereleotris georgegilli* and *H. nebulofasciata* differ from congeners in having the following character combination: scales confined to posterior part of body and caudal peduncle; head pores present; and preopercular pores absent. The two species also have a similar preserved colour pattern. However, *H. georgegilli* differs from *H. nebulofasciata* in having: fewer segmented rays in the second dorsal fin (10–11, usually 10 versus 11); fewer segmented anal-fin rays (9 versus 9–10, usually 10); more pectoral-fin rays (16–18, usually 18 versus 15–16); ctenoid scales (versus cycloid); fifth segmented pelvic-fin ray unbranched and short (versus relatively well-developed, slightly shorter than fourth segmented ray, unbranched or branched once); and a prominent dark spot on the dorsal part of the pectoral fin (lacking in *H. nebulofasciata*).

Hetereleotris georgegilli resembles *H. apora* (Hoese & Winterbottom, 1979) from Mauritius (see below), South Africa, Saint Brandon Shoals, the Comores and the Chagos Archipelago in having: scales ctenoid and confined to caudal peduncle; and fifth segmented pelvic-fin ray reduced (usually absent in *H. apora*). *Hetereleotris apora* differs from *H. georgegilli* in having: two prominent opercular spines (versus spines lacking); fewer lateral scales (4–6 versus 10–13); no head pores (versus head pores present); fewer pectoral-fin rays (15–16 versus 16–18, usually 18); more segmented second dorsal-fin rays (10–11, usually 11 versus 10–11,

usually 10); and more segmented anal-fin rays (9–10, usually 10 versus 9).

REMARKS. Two of the three collections that yielded specimens of *H. georgegilli*, were in surge areas (PCH 95-M23 and PCH 95-M30), and the remaining collection was in an area exposed to tidal currents (PCH 95-M20); all collections were in 4–10 m. Thus, *H. georgegilli* appears to be restricted to shallow subtidal, high-energy habitat.

The tip of the pelvic-fin spine of the cleared and stained paratype of *H. georgegilli* took up alcian blue stain (Fig. 4). Birdsong *et al.* (1988: 197) noted similar blue-staining in *Awaous* and sicydiine gobiids and interpreted 'a fleshy (cartilaginous) tip on each pelvic spine' as a potential synapomorphy of these taxa. However, histological studies in progress by L.R. Parenti and the present author indicate that fin spines of many acanthomorphs stain with alcian blue, but that the blue-staining material is keratin not cartilage.

COMMENTS ON OTHER MAURITIAN HETERELEOTRIS

ECOLOGICAL NOTES. Hoese (1986) recorded two species of *Heteroleotris* from Mauritius, *H. vinsoni* Hoese, 1986 and *H. zanzibarensis* (Smith, 1958). The 1995 collections yielded both of these species and three others: *H. apora* (Hoese & Winterbottom, 1979), *H. georgegilli*, and *H. poecila* (Fowler, 1946). Specimens of *Heteroleotris* were collected at thirteen stations (Table 1). Details for three of the stations (PCH 95-M20, PCH 95-M23 and PCH 95-M30) are provided above in the list of type materials for *H. georgegilli*. Locality and habitat details for the remaining ten stations are as follows:

PCH 95-M1: Bai de la Petite Riviere, off Albion Fisheries Research Centre, around coral bommies on sand and rubble bottom, 0.3–1.9 m.

PCH 95-M5: Bai de la Petite Riviere, just south of Pointe Petite Riviere at north end of Albion public beach, around rocks and patch reefs on sand, rock and rubble bottom, 0–1.5 m.

PCH 95-M9: Albion, Pointe Petite Riviere at end of Avenue Victory, rock pools, 0–1 m.

PCH 95-M10: Bai de la Petite Riviere, off Albion Fisheries Research Centre, 20°12'30"S 57°23'E, boulders on sand and gravel bottom, 10–12 m.

PCH 95-M11: Bai de la Petite Riviere, off Albion Fisheries Research Centre, 20°12'00"S 57°23'E, around coral bommie and adjacent coral, rubble and sand, 9–11 m.

PCH 95-M13: Bai de la Petite Riviere, southwest of Albion Fisheries Research Centre, around coral bommie, 10–11 m.

PCH 95-M18: Bai de la Petite Riviere, off Albion Fisheries Research Centre, just outside reef crest, 20°12'30"S 057°23'30"E, around caves and along 2–3 m dropoff in front of reef platform, 4–8 m.

PCH 95-M22: Trou aux Biches lagoon near boating channel, around coral bommies and patch reefs (mainly *Acropora*) and adjacent sand and rubble, 4–5 m.

PCH 95-M27: Albion, off Pointe Petite Riviere at end of Avenue Victory, 10–11 m.

PCH 95-M32: rocky shore at Bel Air, 20°30'30"S 57°34'30"E, rock pools, 0–1 m.

Despite the limited data, there is some indication of ecological separation of the species (Table 1). Of the 13 stations that yielded specimens of the genus, one had three species, seven had two

Table 1 Number of specimens of *Heteroleotris* collected by the author and associates in Mauritius in 1995. See text for locality and habitat data for each station.

	PCH 95-M station number												
	1	5	9	10	11	13	18	20	22	23	27	30	32
<i>H. apora</i>	–	–	–	1	–	2	3	8	–	–	2	–	–
<i>H. georgegilli</i>	–	–	–	–	–	–	–	4	–	1	–	1	–
<i>H. poecila</i>	–	–	5	–	–	–	–	–	–	–	–	–	5
<i>H. vinsoni</i>	5	2	–	–	–	–	–	–	–	–	–	–	–
<i>H. zanzibarensis</i>	5	1	2	1	1	–	18	2	4	2	–	2	–

species, and five had only one species. Overlap can be largely attributed to a single species, *H. zanzibarensis*; it was collected from a variety of habitats ranging from rock pools to reefs in 0–12 m, and was present at each of the stations that yielded more than one *Heteroleotris* species. The remaining species were collected from more restricted habitats: *H. apora* from around bommies, reef and boulders in 4–12 m; *H. georgegilli* from surge and tidal-current areas in 4–10 m; *H. poecila* from rock pools in 0–1 m; and *H. vinsoni* from around coral bommies and patch reefs in 0.3–1.9 m.

TAXONOMIC NOTES. *Heteroleotris apora*. Hoese & Winterbottom (1979) described *H. apora* (as *Liotes aporus*) from four specimens from Sodwana Bay, South Africa. Winterbottom & Emery (1985) recorded the species from the Chagos Archipelago, and Hoese (1986) recorded it from Saint Brandon Shoals. R. Winterbottom (pers. comm.) has also collected it recently from the Comores. Sixteen specimens collected by the author and associates represent a new record for Mauritius: PCH 95-M10 [USNM 344319 (1 spec.)]; PCH 95-M13 [USNM 344320 (2)]; PCH 95-M18 [BMNH 1997.10.24.3 (1), RUSI 56871 (1), USNM 348368 (1)]; PCH 95-M20 [BMNH 1997.10.24.4–5 (2), RUSI 56872 (2), USNM 344321 (4)]; PCH 95-M27 [BMNH 1997.10.24.6 (1), USNM 344322 (1)]. The Mauritian specimens agree well with the descriptions given by Hoese (1986) and Hoese & Winterbottom (1979), except that the superficial neuromasts are more extensive (cf. their Fig. 2 with Fig. 1). However, this apparent difference is probably not real as superficial neuromasts are easily abraded and often difficult to see.

Heteroleotris poecila. Fowler (1946) described *H. poecila* (in his new monotypic genus *Riukiuia*) based on a specimen from Aguni Shima, Ryukyu Islands. Akihito & Meguro (1981) reported on additional specimens from Japan, and Hoese (1986: 14) extended the range to include Taiwan (two specimens), Grand Comore Island (one specimen) and Sri Lanka (23 specimens). Its range is further extended here to Mauritius based on ten specimens collected by the author and associates: PCH 95-M9 [BMNH 1997.10.24.7–8 (2 specs), RUSI 56873 (1), USNM 344333 (2)] and PCH 95-M32 [BMNH 1997.10.24.9 (1), RUSI 56874 (1), USNM 344334 (3)].

Hoese (1986) noted slight differences in pectoral-fin ray number between the Pacific and Indian Ocean specimens: 16–18 with a strong mode of 17 for Indian Ocean specimens versus 16 or 17 with a weak mode of 16 for Pacific Ocean specimens. The following counts were observed in the Mauritian specimens (adult specimens checked only; bilateral counts included): 17 f1; 18 f13. More materials are needed to determine the systematic significance of the relatively high numbers of pectoral-fin rays in the Mauritian specimens. The specimens agree in all other respects with the descriptions provided by Akihito & Meguro (1981) and Hoese (1986).

Heteroleotris vinsoni. Hoese (1986) described *H. vinsoni* from the holotype and 14 paratypes from Mauritius, and from two paratypes from Saint Brandon Shoals; he also listed a non-type specimen from Mozambique. Seven specimens were collected by the author and associates in Mauritius in station PCH 95-M1 [BMNH 1997.10.24.10

–11 (2 specs), RUSI 56875 (1), USNM 344318, (2)] and PCH 95-M5 [USNM 348369 (2 specs)]. The specimens agree well with Hoese's original description and figures of the species. (Note that Hoese's Fig. 5 of the cephalic laterosensory system of this species has been inadvertently swapped with his Fig. 3 for *H. margaretae*.)

Heteroleotris zanzibarensis. Smith (1958) described *H. zanzibarensis* from a specimen from Zanzibar (as a new genus and species of eleotrid(id), *Satulinus zanzibarensis*); later (Smith, 1959) he described the species a second time (as a new species of gobiid, *Monishia oculata*) from specimens from Mahé, Seychelles (type locality), Kenya and Mozambique. Hoese (1986) extended its range to include the Agelega Islands, Saint Brandon Shoals and Mauritius, and R. Winterbottom (pers. comm.) has recently collected it at the Comores. Thirty-eight specimens were collected by the author and associates in Mauritius: PCH 95-M1 [BMNH 1997.10.24.12–13 (2 specs), RUSI 56876 (1), USNM 344323 (2)]; PCH 95-M5 [USNM 344324 (1)]; PCH 95-M9 [USNM 344325 (2)]; PCH 95-M10 [USNM 344326 (1)]; PCH 95-M11 [USNM 344327 (1)]; PCH 95-M18 [BMNH 1997.10.24.14–18 (5), RUSI 56877 (4), USNM 344328 (9)]; PCH 95-M20 [BMNH 1997.10.24.19 (1), USNM 344329 (1)]; PCH 95-M22 [BMNH 1997.10.24.20 (1), RUSI 56878 (1), USNM 344330 (2)]; PCH 95-M23 [USNM 344331 (2)]; PCH 95-M30 [USNM 344332 (2)].

Hoese (1986) noted that *H. zanzibarensis* varies considerably in the development of the pelvic-fin disc, with some specimens possessing a complete disc (i.e., with a low fraenum connecting the spine bases and a membrane connecting the fifth segmented rays) and others possessing barely united pelvic fins (i.e., no apparent fraenum between spine bases and fifth segmented rays connected only at their bases). This variation led Smith (1958, 1959) to place *Satulinus zanzibarensis* and *Monishia oculata* in separate families; until recently, development of the pelvic-fin disc was the primary basis for separation of the Gobiidae from the Eleotrididae. The Mauritian specimens examined here agree well with the pelvic-fin variation noted by Hoese (1986); approximately half of the specimens have a completely developed disc and the remainder have incompletely united fins.

Hoese (1986) noted highly variable pectoral-fin-ray counts for *H. zanzibarensis*. Similar highly variable counts were noted for the Mauritian specimens examined here. Bilateral counts recorded from a subsample of the specimens were: 16 f7; 17 f19; 18 f6.

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Revision of *Schismatorhynchos* Bleeker, 1855 (Teleostei, Cyprinidae), with the description of two new species from Borneo

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CONTENTS

Introduction	97
Materials and Methods	98
Generic Account	98
<i>Schismatorhynchos</i> Bleeker, 1855	98
Species Accounts	100
Key to the species of <i>Schismatorhynchos</i>	100
<i>Schismatorhynchos heterorhynchos</i> (Bleeker, 1853)	100
<i>Schismatorhynchos holorhynchos</i> sp. nov.	104
<i>Schismatorhynchos endecarhapis</i> sp. nov.	105
Intrageneric comparisons	107
Discussion	107
Annotations to keys of cyprinid genera of the region	108
Acknowledgements	108
References	108

SYNOPSIS. *Schismatorhynchos* Bleeker, 1855 is revised: the genus is enlarged to accommodate two new species from Borneo, *Schismatorhynchos endecarhapis* n. sp. is described from the Kapuas and Barito rivers, Kalimantan Barat and Kalimantan Tengah and *Schismatorhynchos holorhynchos* n. sp. is described from the Rejang and Kinabatangan rivers Sarawak and Sabah, Malaysia. *Schismatorhynchos* is characterised by oro-labial features, namely the upper lip not continuous with the lower lip around the corner of the mouth, a wide crescentic lower jaw, the lower jaw lightly armoured with a thin, flexible, keratinous cutting edge and a lower labial frenulum in which the mandibular laterosensory canal is located. Only *S. heterorhynchos* (Bleeker, 1853), the type species, possesses the eponymous rostral cleft. *Nukta* Hora, 1942 is excluded from *Schismatorhynchos* on the grounds it lacks the specialisations of the three Sundaland species. A key to species in the genus is provided and annotations to currently used regional keys to cyprinid genera are suggested in order to accommodate an enlarged *Schismatorhynchos*.

INTRODUCTION

The cyprinid genus *Schismatorhynchos* Bleeker, 1855, with a disjunct distribution in Sumatra–Borneo and India, is known by a strange rostral modification, a heavily tuberculate snout with a deep horizontal cleft (Bleeker, 1853; Weber & de Beaufort, 1916; Hora, 1942). Two species, each in separate subgenera, are currently included in *Schismatorhynchos*, *S. (Schismatorhynchos) heterorhynchos* (Bleeker, 1853) from Sumatra and Borneo and *S. (Nukta) nukta* (Sykes, 1841) from India. In addition to its unusual snout the nominate subgenus is also known for unusual oro-labial morphology which includes: 1) a frenulum connecting the lower lip to the anterior gular region; and 2) a lower jaw with an elongated cutting edge which separates the upper lip from the lower lip at the corners of the mouth – the lips are not continuous around the corner of the mouth (Weber & de Beaufort, 1916). Since the description of the subgenus *Nukta* by Hora (1942) *Schismatorhynchos* has received little attention except for listing in faunal reviews.

Schismatorhynchos heterorhynchos was described from Sumatra (Bleeker, 1853) and Weber & de Beaufort (1916) reported it elsewhere only from the Kapuas River, western Borneo. More recently, Inger & Chin (1962) identified juvenile specimens from the Kinabatangan River, Sabah, Malaysia (northeastern Borneo) as *S. heterorhynchos* (Bleeker, 1853) even though this northeastern Borneo material lacks a cleft snout. Since the Sabah specimens lack tubercles on the snout in the region of the cleft in the snout of *S. heterorhynchos*, and since *S. heterorhynchos* was known only from larger specimens, Inger & Chin implied that the cleft in the snout might not develop until maturity. Roberts (1989; Fig. 58) also identified some juvenile material without a cleft snout, but from the Kapuas River, western Borneo, as *S. heterorhynchos*. The oro-labial morphology of the subgenus *Schismatorhynchos* is apparently so distinctive that both Inger & Chin (1962) and Roberts (1989) were able to identify material as belonging to it even in the absence of the eponymous rostral cleft.

We collected juveniles of an unusual fish with a distinctive colour

pattern from the upper part of the Barito River basin, Kalimantan Tengah, Indonesia (central Borneo) in Jan–Feb 1991, and a larger specimen was taken subsequently in July 1992, again from the upper part of the basin. The species proved difficult to identify to genus, with a dorsal fin branched ray count of 11, a modal count of 33 lateral-line scales, the upper and lower lips not continuous around the corner of the mouth, and an undivided, moderately tuberculate snout. This Barito River material appeared identical to the illustration of a specimen from the Kapuas River identified as *S. heterorhynchus* by Roberts (1989; Fig. 58). Examination of Kapuas materials deposited by Roberts in the Museum Zoologicum Bogoriense confirmed that the Barito materials are conspecific with the Kapuas specimen Roberts illustrated. However, the disparity in the counts of branched rays of the dorsal fin between the Barito–Kapuas materials and that of *S. heterorhynchus* (eight branched rays in the dorsal fin), and differences in colour pattern, led us to conclude that the Sabah and Sarawak materials do not conform to *S. heterorhynchus*, but instead are from a previously unrecognised species of *Schismatorhynchus*.

In order to investigate the development of the snout cleft in *S. heterorhynchus*, we examined small specimens from northeastern Borneo identified as *S. heterorhynchus* (see Inger & Chin, 1962), along with additional material collected in 1991 in Sarawak, Malaysia. Differences in snout tubercle structure and colour pattern led us to conclude that the Sabah and Sarawak materials do not conform to *S. heterorhynchus* either, but instead belong to yet another unrecognised species.

More material has become available recently from the Kapuas River, western Borneo (Sungei Sibau, an upper basin tributary of the Kapuas River). This material possesses, even as juveniles of small size, the oro-labial features of *S. (Schismatorhynchus)*, a deeply cleft heavily tuberculate snout and a colour pattern like that described for *S. heterorhynchus*. Thus, at least two species of *Schismatorhynchus* live within the Kapuas River basin, one species with a cleft snout and another with an undivided snout.

To summarise our observations and clarify the status of material identified in the literature as *S. heterorhynchus*, we revise the genus *Schismatorhynchus*, describing two new species.

MATERIALS AND METHODS

Methods of measuring and counting follow Hubbs and Lagler (1949). Vertebral (following Siebert & Guiry, 1996) and fin-ray counts were taken from radiographs. Statistical analyses were carried out using SYSTAT for WINDOWS, version 6.0 (SPSS, Inc. 1994). Institutional abbreviations are as follows: BMNH – The Natural History Museum, London; FMNH – The Field Museum of Natural History, Chicago; MZB – Museum Zoologicum Bogoriense, Bogor; USNM – United States National Museum of Natural History, Washington, D.C.; ZMA – Zoological Museum, Amsterdam.

The systematics and generic taxonomy of cyprinid fishes related to *Labeo* Cuvier, 1817, i.e. those with a vomero-palatine organ, is in a state of flux and is likely to remain so for some time to come. There is considerable disagreement in the modern analytical literature as to what subgroups should be recognised, just what their limits ought to be, and at what rank they should be recognised (compare Reid (1985; Table 1, p. 15) with Rainboth (1996; p. vii) to see conflict at all the levels just mentioned). As regards this revision of *Schismatorhynchus*, we adopt Rainboth's rank of tribe for the entire group of cyprinids with a vomero-palatine organ, and use the informal name labeonin when referring to them in a general way. We

accept Reid's restriction of *Labeo*, and, for the most part, his notions of relationships within labeonins when discussing the limits of *Schismatorhynchus*, because his groupings have been laid out following cladistic principles. We use *Tylognathus* Heckel (*sensu* Bleeker, 1863; Reid, 1985, p. 277) when discussing our exclusion of *Nukta* Hora from *Schismatorhynchus* because we are not sure of the limits of *Bangana* Hamilton. *Cyprinus nukta* Sykes, 1838 may belong in *Bangana*, but that assessment is beyond the scope of this study.

GENERIC ACCOUNT

Schismatorhynchus Bleeker, 1855

Schismatorhynchus Bleeker, 1863; unjustified emendation.

Type species *Lobocheilus heterorhynchus* Bleeker, 1853; type by monotypy.

DIAGNOSIS. Labeonins (*sensu* Reid, 1982, 1985; 1. vomero-palatine organ present, 2. neural complex of the Weberian apparatus in direct contact with supraoccipital region, 3. terete process of the basioccipital, 4. superficial labial fold developed posterior to the lower jaw) with a large, fleshy, sub-conical, rostral cap (=rostral fold of Weber & de Beaufort, 1916); two pairs of barbels, posterior pair in a deep recess at the corner of the mouth (largely to completely hidden in large material); mouth inferior, wide, C-shaped; lower jaw with an extremely long, thin, flexible, horny, cutting edge (Fig. 1A–C); no superficial labial fold in advance of the upper jaw; upper lip separated from rostral cap, moderately fleshy, adnate to upper jaw; upper lip and lower lip not continuous around corner of mouth (separated by extensions of the cutting edge of lower jaw); lower lip reflected from lower jaw, thick, very fleshy, fringed, with a distinct, elongate, longitudinally oriented, fleshy, lateral lobe in which the mandibular laterosensory canal is located (=frenulum of Weber & de Beaufort, 1916; Fig. 1A–C); no transverse postlabial groove separating lower lip from gular region.

REMARKS. The present diagnosis makes use of many oro-labial features and excludes the subgenus *Nukta* from *Schismatorhynchus*. Additional information on the oro-labial features is presented below, with an explanation of our exclusion of *Nukta*.

Good series of small individuals are available for both new species, making possible study of certain aspects of the late ontogeny of the mouth. *Schismatorhynchus* is a labeonin, as delimited by Reid (1982, 1985). It appears to lack the superficial labial fold anterior to the upper jaw that characterises a large subgroup of these fishes, such as *Garra*, *Epalzeorhynchus*, *Osteochilus*, and *Labeo*. At small size (< 30 mm SL) the upper lip is distinguishable as a ridge of papillate tissue closely associated with the upper jaw. This ridge thickens and becomes fully adnate to the upper jaw with growth, so that by a size of 50 mm SL no distinction between the upper jaw and upper lip is apparent, unlike members of the subgroup of labeonins, such as *Epalzeorhynchus*, with a scarcely developed, or regressed, but nevertheless distinguishable superficial labial fold anterior to the upper jaw. Thus, *Schismatorhynchus* appears to reside within a relatively primitive assemblage of labeonin genera, which includes *Tylognathus* (*sensu* Bleeker, 1963; Reid, 1985; p. 287) and *Lobocheilus*, but for which relationships have yet to be worked out.

More clear is that the extremely elongate cutting edge of the lower jaw, which results in the separation of the upper and lower lips around the corner of the mouth, and the development of a lateral frenulum are distinct specialisations within labeonins and unique among cyprinids. These oro-labial specialisations of *Schismo-*

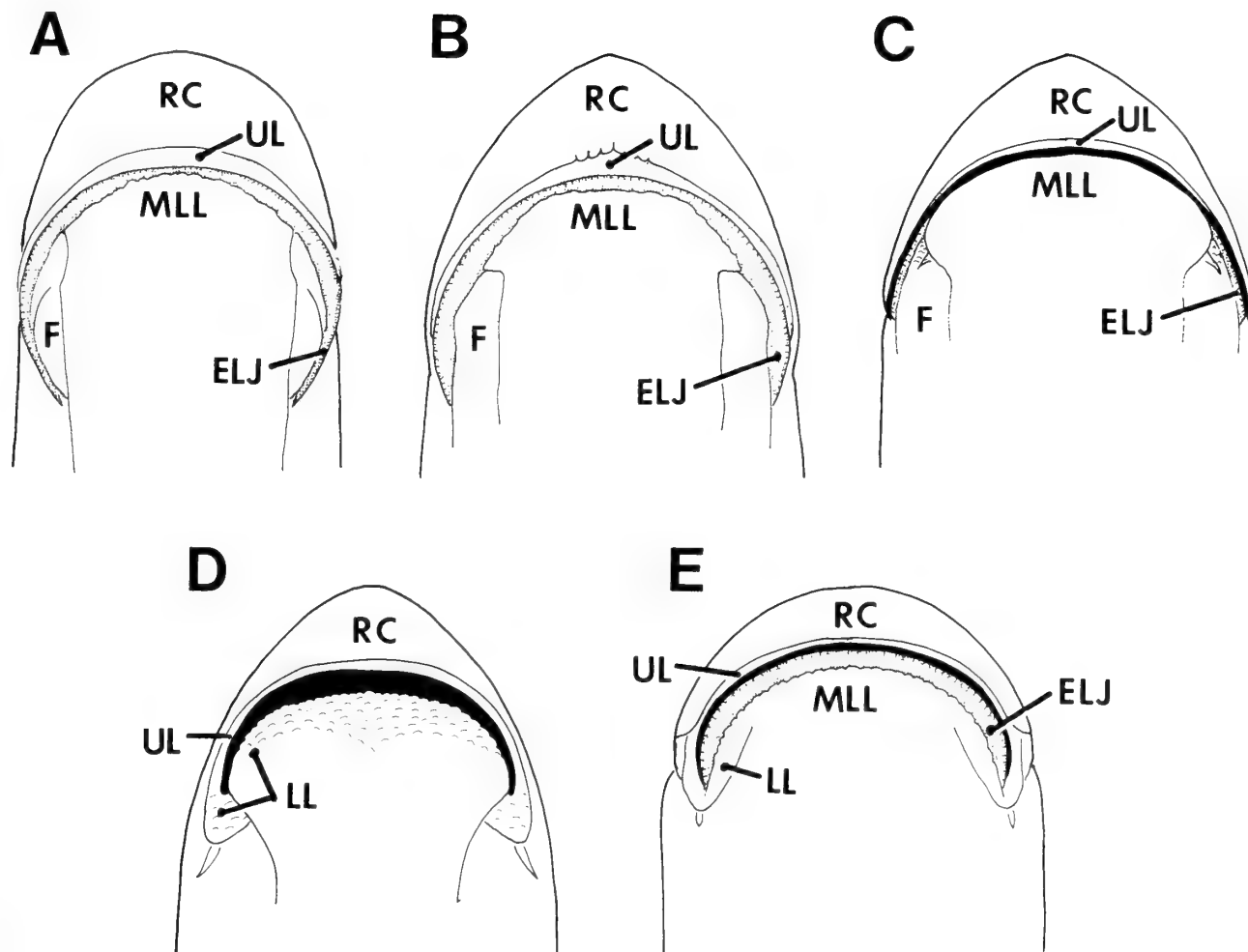


Fig. 1 Outline drawings of oro-labial structure of: A. *S. heterorhynchos*, MZB unregistered, mm SI; B. *S. holorhynchos*, USNM 325389, 101.7 mm SI; C. *S. endecarhapis*, MZB 6092, 179.0 mm SI; D. *Lobocheilos bo*, BMNH 1993.5.19:1, 87.0 mm SI; E. *Tylognathus diplostomus*, BMNH 1932.2.20:7, 215.0 mm SI. ELJ=edge of lower jaw; F=frenulum; LL=lower lip; M=mouth; MLL=median lobe lower lip; PG=postlabial groove; RC=rostral cap; UL=upper lip.

rhynchos develop from structure general for labeonin cyprinids, exemplified by *Tylognathus diplostoma* (Heckel, 1838) (Fig. 1E) and similar to that of *Tylognathus nukta* (Hora, 1942: Fig. 9b; see Reid, 1985: p. 287 for the assignment of *Labeo nukta* to *Tylognathus*). At < 30 mm SI oro-labial structure of individuals of *Schismatorhynchos* is like that of *T. diplostoma* or *T. nukta*. At about 30 mm SL the cutting edge of the lower jaw elongates, eventually interrupting the connection between the upper and lower lips around the corner of the mouth. At about the same time the fold in the skin which separates the region of the mandibular laterosensory canal from the rest lower labial tissue deepens, eventually forming the structure Weber & de Beaufort (1916) referred to as the frenulum. Rather than connecting the lower lip to the gular region, this frenulum houses the mandibular laterosensory canal. As the cutting edge of the lower jaw elongates, the portion of the lower lip between the lateral edge of the lower lip and the principle lobe of the lower lip regresses, completely in the two new species, nearly so in *S. heterorhynchos*.

Elongation of the cutting edge of the lower jaw progresses farther in *S. holorhynchos* and *S. heterorhynchos* and their mouths are more crescentic than that of *S. endecarhapis*; they are probably each other's closest relative.

Nukta Hora is considered by some recent authors to be a synonym of *Schismatorhynchos* (Jayaram, 1981; Eschmeyer & Bailey, 1990; Talwar & Jhingran, 1991). We do not agree with this assessment. Instead we follow Reid (1985), insofar as his exclusion of *Nukta* from *Schismatorhynchos*, and our diagnosis excludes *Nukta* from *Schismatorhynchos*. Our reasons for supporting Reid are elaborated below.

Hora (1942) erected *Nukta* as a subgenus of *Schismatorhynchos* for *T. nukta* (Sykes, 1841) in order to call attention to 'the great similarity in the form of [*S. heterorhynchos* and *T. nukta*]', by which he meant that both possess a deeply incised, heavily tuberculate snout, the upper lobe of which forms a projection from between the eyes. However, the outcome of the comparison between *S. heterorhynchos* and *T. nukta* was not straightforward.

Whilst wishing to stress the similarity in the form of the snout between the two species, Hora also recognised that they differ so greatly in oro-labial structure that he also wrote 'differences . . . in the structure of the lips and associated structures are of sufficient value to separate the two species generically'. Hora resolved the dilemma between the similarity in the form of the snout and the difference in oro-labial structure by subordinating *Nukta* under *Schismatorhynchos*.

At the time *Nukta* was erected only *S. heterorhynchus* was known and a direct comparison between it and *T. nukta* was logical. The discovery of additional species with the oro-labial specialisations of *S. heterorhynchus* complicates the issue. Hora's phyletic association focused on the remarkably modified snout found in each species but the discovery of species of *Schismatorhynchus* with unmodified snouts renders the association untenable because either the new *Schismatorhynchus* species would have had to regress to an unmodified snout condition from the modified condition of *S. heterorhynchus* and *T. nukta* or *T. nukta* would have had to regress to an unspecialised oro-labial condition from the specialised condition of *Schismatorhynchus*. Either possibility is more complex, and therefore deemed less likely, than the explanation required when just *S. heterorhynchus* and *T. nukta* were known.

Hora, in making the comparison between *S. heterorhynchus* and *T. nukta*, was, in part, acting on the suggestion by Weber & de Beaufort (1916) that *Schismatorhynchus* might also be present on the Indian subcontinent, though they presented no evidence to support this suggestion. Hora's comprehensive knowledge of the Indian fish fauna led him to conclude that the only species Weber & de Beaufort could possibly have been referring to was *T. nukta*. However, they may have been simply following Bleeker (1853, 1855), who noted in his description of *S. heterorhynchus* that two Indian species illustrated in Gray (1830, 1832) appeared to have snouts similar in structure to the species he was describing. Bleeker listed *Cyprinus gotyla* Gray, 1830 (= *Garra gotyla*) and *Cyprinus falcatus* Gray, 1832 (= ?*Tylognathus falcatus*; not *Tylognathus diplostomus* (Heckel, 1838) nor *T. dycocheilus* (McClelland, 1839)). The conclusion by Hora (1942:11) that Weber & de Beaufort could only have been referring to *T. nukta* may well have been mistaken, and may have led to a comparison they, nor Bleeker, ever intended.

The discovery of two additional labeonin species with oro-labial morphology like that of *S. heterorhynchus* demonstrates *T. nukta* is not the closest relative of *S. heterorhynchus*. This and Bleeker's reference to the snout of species other than *T. nukta* brings the character of a divided snout into sharp focus.

A heavily tuberculate snout commonly occurs among labeonins, as does the separation of the ethmoidal region from the premaxillary-maxillary region by creases, folds, and indentations in the skin. In some cases these are deep enough to 'divide' the snout. Since the condition occurs widely, and sporadically among labeonins its status as a synapomorphy in any particular case must be confirmed by congruence with other characters. In the case of *S. heterorhynchus* and *T. nukta* the requirement of corroboration from additional characters is not met. Rather, the oro-labial specialisations common to all species of *Schismatorhynchus* suggest any resemblance between the divided snout of *S. heterorhynchus* and *T. nukta* is one of convergence, and therefore without taxonomic significance.

In summary, we support Reid's exclusion of *Nukta* from *Schismatorhynchus* for three reasons: the oro-labial specialisations of *Schismatorhynchus* are unique among cyprinids; the 'divided' snout of *S. heterorhynchus* and *T. nukta* is not corroborated as a useful indicator of relationship; and Hora was probably mistaken when he assumed Bleeker and Weber & de Beaufort were suggesting a comparison between *S. heterorhynchus* and *T. nukta*. Subordinating *Nukta* within *Schismatorhynchus* renders *Schismatorhynchus* polyphyletic. Restricting *Schismatorhynchus* to Bleeker's and Weber & de Beaufort's concept of a group of labeonins with an elongate lower jaw cutting edge which separates the upper lip from the lower lips at the corner of the mouth, and also with a lower labial frenulum which houses the mandibular laterosensory canal, exactly matches Hora's concept (1942:12–13) for the nominate subgenus *Schismatorhynchus*.

SPECIES ACCOUNTS

An account of each species of *Schismatorhynchus* is presented below, and a comparative account for all three is given at the end of the section.

Key to the species of *Schismatorhynchus*.

- 1a. Snout with horizontal cleft, dark lateral band extends to the distal tips of middle caudal fin-rays *S. heterorhynchus*
- 1b. Snout without horizontal cleft, middle caudal fin-rays not pigmented Go to 2
- 2a. Dorsal fin branched ray count > 9 *S. endecarhapis* sp. nov.
- 2b. Dorsal fin branched ray count < 10 *S. holorhynchus* sp. nov.

Schismatorhynchus heterorhynchus (Bleeker, 1853)

(Figs 1A,2,3A,5)

Lobocheilos heterorhynchus Bleeker, 1853: 524.

Schismatorhynchus lobocheiloides Bleeker, 1855: 259.

Schismatorhynchus heterorhynchus Bleeker, 1863: 193.

Tylognathus heterorhynchus Gunther, 1867: 67.

SYNTYPE. BMNH 1866.5.2.82 (143.3 mm SL), [Indonesia], Sumatra, Solok, H.C. Schwanenfeld.

NON-TYPE MATERIALS. Sumatra – ZMA 115.911 (5, 175–228 mm SL); [Indonesia]; Sumatra, Penetai, E. Jacobson, VII-1915. MZB 4818 (2, 119.6–156.6 mm SL); Indonesia; Sumatra, Jambi Province; Batang Hari basin, Sungai Meringin at Muaraimat; col. Suroto and M. Siluba; 16-VIII-1982.

Borneo (Kapuas River basin, Kalimantan Barat, Indonesia) – MZB 5456 (2; 67.9–71.2 mm SL), Sungai Kapuas at Putussibau, col. Munandar, 26-IV-1983. Upper part of Sungai Sibau, col. Ike Ratchmatica and Haryono, 25 June–7 July 1996: 1) MZB 8600, Station IV (1, 98.8 mm SL); 2) MZB 8601, Station IV, Habitat 2 (1, 110.4 mm SL); 3) MZB 8602, Station VI.2 (2, 86.9–97.6 mm SL); 4) MZB 8603, Station IX, at Muara Suluk (1, 134.0 mm SL); 5) MZB 8604, Station XIII (5, 85.4–93.8 mm SL); and 6) MZB 8605, Station XIV, at Muara Apeang (1, 101.7 mm SL). Sungai Putan, an upper basin tributary of Sungai Sibau; col. Ike Ratchmatica and Haryono; 22–26 Jun 1996: 1) MZB 8606, Station III (2, 91.7–93.3 mm SL); 2) MZB 8607, Station IV (1, 106.6 mm SL); 3) MZB 8608, Station V (1, 107.3 mm SL); 4) MZB 869, Station VIII (2, 89.4–96.0 mm SL); and 5) MZB 8610, Station VI (1; 92.2 mm SL). Sungai Apeang, an upper basin tributary of Sungai Sibau; col. Ike Ratchmatica and Haryono; 30 Jun 1996: 1) MZB 8611, Station X.2 (2, 98.6–128.2 mm SL); and 2) MZB 8612, Station X.4 (2, 104.8–136.9 mm SL). Sungai Aring, an upper basin tributary of Sungai Sibau; col. Ike Ratchmatica and Haryono; 7 Jul 1996: 1) MZB 8613, Station XVI (1, 96.2 mm SL); and 2) MZB 8614, Station XVI.2 (3, 97.2–131.0 mm SL). Sungai Menjakan, an upper basin tributary of Sungai Sibau; col. Ike Ratchmatica and Haryono, 1 Jul 1996: 1) MZB 8615, Station XI.1 (1, 132.6 mm SL); and 2) MZB 8616, Station XI.3 (1, 81.4 mm SL). Sungai Sekedam Besar, an upper basin tributary of Sungai Sibau; col. Ike Ratchmatica and Haryono; 25 June 1996, MZB 8617, Station II (3, 09.1–97.6 mm SL). Sungai Berarap, an upper basin tributary of Sungai Sibau; col. Ike Ratchmatica and Haryono; 3 Jul 1996; MZB 8618, (1, 95.0 mm SL).

DIAGNOSIS. A species of *Schismatorhynchus* with a deep horizontal cleft in snout (*S. holorhynchus* and *S. endecarhapis* without cleft in snout); snout, including cleft, heavily tuberculate, tubercles pyra-

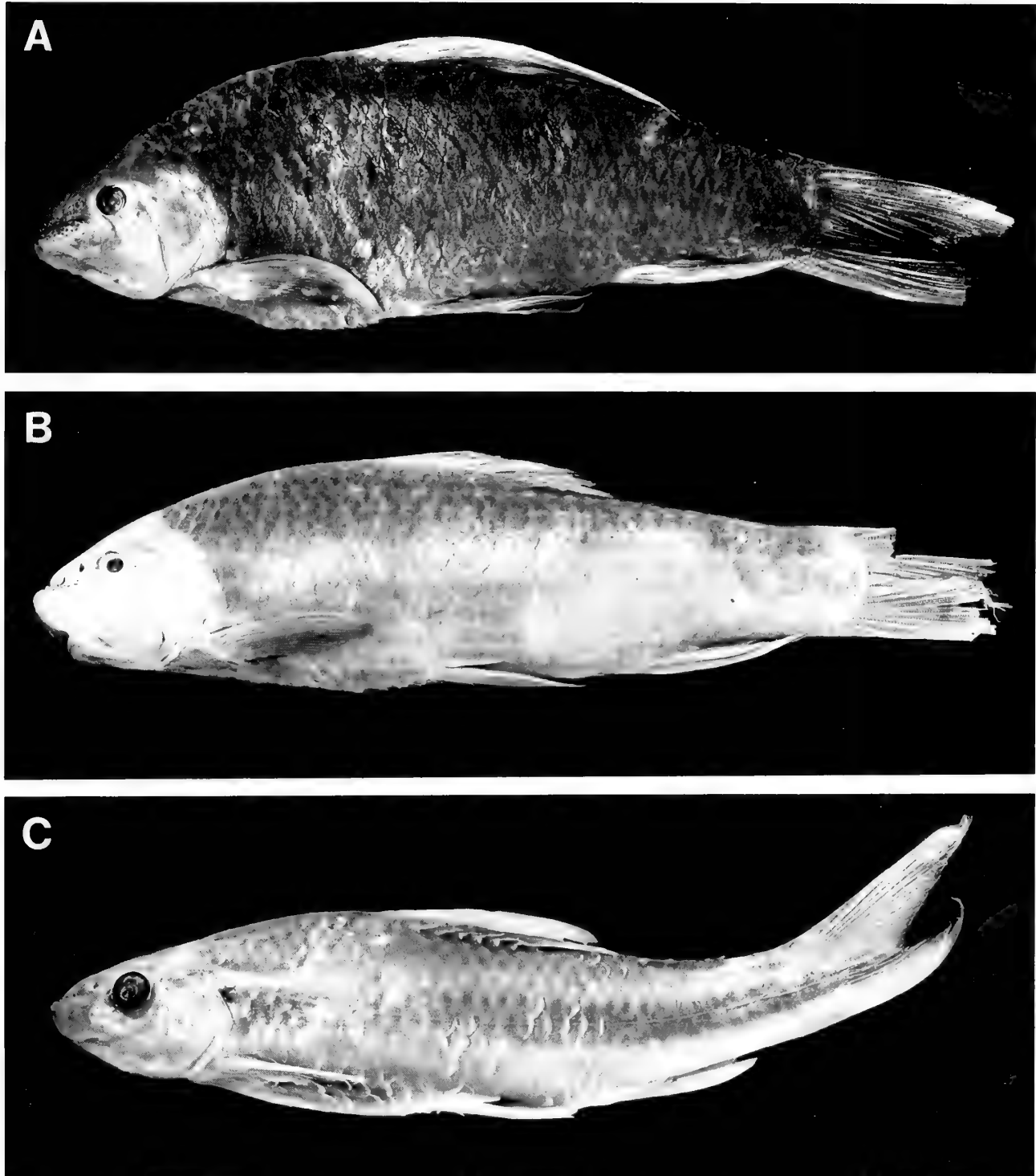


Fig. 2 Photograph of a large (A. ZMA 115.911, 224 mm SL), medium (B. syntype, BMNH 1866.5.2.82, 143.3 mm SL), and small (C. MZB 5456, 68.8 mm SL) specimens of *S. heterorhynchus*.

midal, large, unicuspid (*S. holorhynchus* with conical, multi-cuspidate tubercles; *S. endecarhapis* with simple, conical tubercles); dorsal fin with eight branched fin-rays, falcate, anterior two principle fin-rays very elongate in larger individuals (*S. endecarhapis* with 11 branched rays in dorsal fin); distinct, dark lateral band extending to distal tips of middle rays of caudal fin (lateral band of *S. holo-*

rhynchus and *S. endecarhapis* not extending onto caudal fin-rays).

DESCRIPTION. Material in a 70–225 mm SL size range was available for study. No material was available below 68 mm SL and the five largest specimens are not in good condition. They are old, poorly preserved, and flattened, limiting study of shape change in

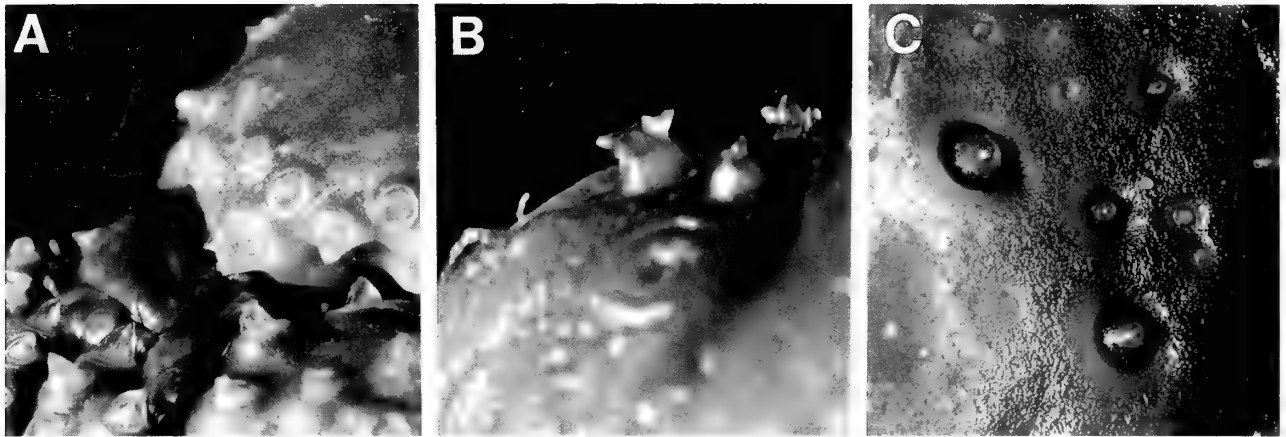


Fig. 3 Snout tubercles of: A. *S. heterorhynchus*, MZB 8612, 136.4 mm SL; B. *S. holorrhynchus*, FMNH 68550, 77.6 mm SL; C. *S. endecarhapis*, MZB 6092, 179.0 mm SL.

this species, which appears considerable. A photograph of a small, medium and large specimen is presented in Figure 2. Selected morphometric ratios, meristic information, and vertebral counts are reported in Tables 1–3.

Head relatively long, with a comparatively small eye, increased head length due to an elongate, pointed snout with a well developed rostral fold (=rostral cap of Roberts, 1989) which is hypertrophied in support of heavy tuberculation. Snout divided by a deep horizontal cleft above 1st infraorbital bone (Io 1). Upper (ethmoidal) lobe consists of connective tissue outgrowth from front edge of mesethmoid, supports large tubercles; in dorsal view its anterior edge indented in midline to form left and right anterior lobes. Anterior extension of rostral cap also consists of a connective mass which supports anterior tubercles of snout. Two pairs of barbels present, anterior pair small, posterior pair longer, but hidden in a deep recess at corner of mouth.

Mouth inferior, broad, C-shaped, usually a little wider than long (mean Mw:MI = 1.3; range = 0.9–1.6., SE = 0.05, n=32). Lower jaw equipped with an emergent, thin, flexible, extremely long cornified cutting edge which is much longer than posterior extent of upper and lower lips. Posterior tips of cutting edge of lower jaw extend behind a vertical line from middle of eye.

Large, unicuspid, pyramidal tubercles, with 3–5 sides, present in and around rostral cleft (Fig. 3A). Tubercles also present around dorsal edges of upper lobe of snout formed by rostral cleft, on upper and lower interior surfaces of rostral cleft, between eye and nares, on upper half of Io 1, and over dorsal and anterior aspects of rostral cap. Large tubercles absent from dorsal surface of head except for those found at dorsal edges of upper lobe of snout.

Shape of *S. heterorhynchus* changes with size (Fig. 2). Smallest

specimens examined have a relatively round body. Between 100 mm SL and 150 mm SL body depth and compression increases. Above 170 mm SL body shape is deep and decidedly compressed.

Dorsal fin falcate, with first two principal fin-rays greatly elongated in large individuals, when depressed extending beyond anal-fin origin to more than mid-way along caudal peduncle. Dorsal fin height nearly 50% of SL in largest individuals examined. Increase in length of first two principal dorsal-fin rays strongly allometric with respect to SL, with allometric coefficient much greater than unity (Fig. 4). Pectoral fin of large individuals slightly longer than head length, but in small individuals much shorter than head length. Pelvic fin inserted behind dorsal-fin origin, at 4th branched ray of dorsal fin.

Lateral line usually with 31 or 32 scales (Table 2) to end of hypural plate, slightly curved, running in middle of caudal peduncle posteriorly; 5½ scales above lateral line to dorsal origin; 4½ scales below lateral line. All specimens examined with 31 vertebrae, usually with 15 precaudal vertebrae and 16 caudal vertebrae (Table 3). Number of pairs of pleural ribs usually 12.

In alcohol dorsum dark, with ventral half of body creamy. A wide, dark lateral band present, centred on lateral line, beginning at operculum and extending to distal tips of middle rays of caudal fin. Upper anterior corner of lateral stripe, where it meets hind edge of operculum, intensified to form a dark mark, prominent in smaller individuals but less so in larger individuals. Lateral band two scale rows wide, includes lower ½ of scale row above lateral line scale row and upper ½ of scale row below lateral line scale row. Lateral band may be evident only on the posterior half of the body on large individuals. Dorsal, pectoral, pelvic, anal, and upper and lower lobes of caudal fin clear.

Table 1 Selected morphometric variables for species of *Schismatorhynchus*; the mean is followed (±) by the standard deviation; the range is reported as the minimum and maximum observation; sample size is reported in column headings.

	<i>S. heterorhynchus</i> n=38	<i>S. holorrhynchus</i> n=81	<i>S. endecarhapis</i> n=19
Head length	26.6±1.4 22.6–28.9	25.4±1.2 21.5–27.7	24.5±1.4 20.5–27.0
Snout length	12.5±1.1 10.8–14.2	9.6±1.0 6.9–11.2	8.7±0.9 6.9–10.2
Eye length (%HL)	18.6±1.8 13.5–20.8	22.3±2.8 17.7–28.8	23.1±3.4 18.3–30.8
Eye length	4.9±0.6 3.4– 6.0	5.9±0.8 4.4– 7.4	5.7±1.0 4.1– 7.7
Predorsal length	47.6±1.5 43.6–50.4	47.8±2.2 39.2–52.8	47.7±1.4 45.5–50.2
Body depth	27.0±2.9 21.9–35.6	27.5±1.7 23.0–30.5	25.0±1.9 21.4–28.6
Caudal peduncle depth	12.4±1.0 11.0–15.4	12.8±0.6 11.2–13.8	11.1±0.5 10.2–12.2
Dorsal-fin base length	17.7±1.6 12.4–22.3	16.1±1.1 12.4–18.9	24.6±1.8 22.4–29.3

Table 2 Lateral line scale count frequencies for species of *Schismatorhynchus*.

	30	31	32	33	34
<i>S. heterorhynchus</i>	4	12	18	4	
<i>S. holorhynchus</i>	4	50	9	3	
<i>S. endecarhapis</i>			3	13	3

DISTRIBUTION. Studied material of *S. heterorhynchus* originates from three localities on Sumatra and from the Kapuas River basin, Kalimantan Barat, Borneo (Fig. 5). We consider only the two most recent reported Sumatra localities to be verifiable. Solok is reported as the type locality of the species (Bleeker, 1853), but we are not confident the types actually originate from there. Solok is located in the very upper reaches of the Indragir River basin Sumatera Barat Province, just north of the Batang Hari basin and on the overland route between the cities of Jambi, Jambi Province and Padan, Sumatera Barat Province. Much of this route is in the Batang Hari basin and it is quite possible the material Bleeker listed as coming from Solok was actually collected along the route to Solok and within the Batang Hari basin. Within the Kapuas River basin verified localities at which *S. heterorhynchus* has been captured are all within the Sungai Sibau basin. *Schismatorhynchus heterorhynchus* has been collected only from the upper parts of river basins, near to or in foothill regions, both on Sumatra and Borneo. These parts of river basins are among the least well collected and further exploration of these habitats may reveal the species to be quite widespread.

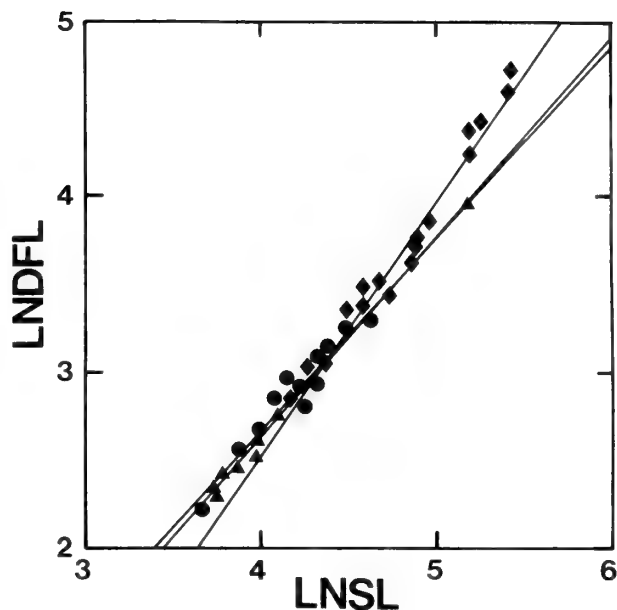


Fig. 4 Log-log plot (natural logarithms) of the relationship between height of the dorsal fin and standard length; \blacklozenge = *S. heterorhynchus*, $\text{LnDfL} = -3.2 + 1.44\text{LnSL}$, SE of coefficient = 0.05, $R^2 = 0.96$, $n = 36$; \blacktriangle = *S. endecarhapis*, $\text{LnDfL} = -1.7 + 1.09\text{LnSL}$, SE of coefficient = 0.07, $R^2 = 0.92$, $n = 25$; and \bullet = *S. holorhynchus*, $\text{LnDfL} = -1.9 + 1.12\text{LnSL}$, SE of coefficient = 0.04, $R^2 = 0.99$, $n = 13$.

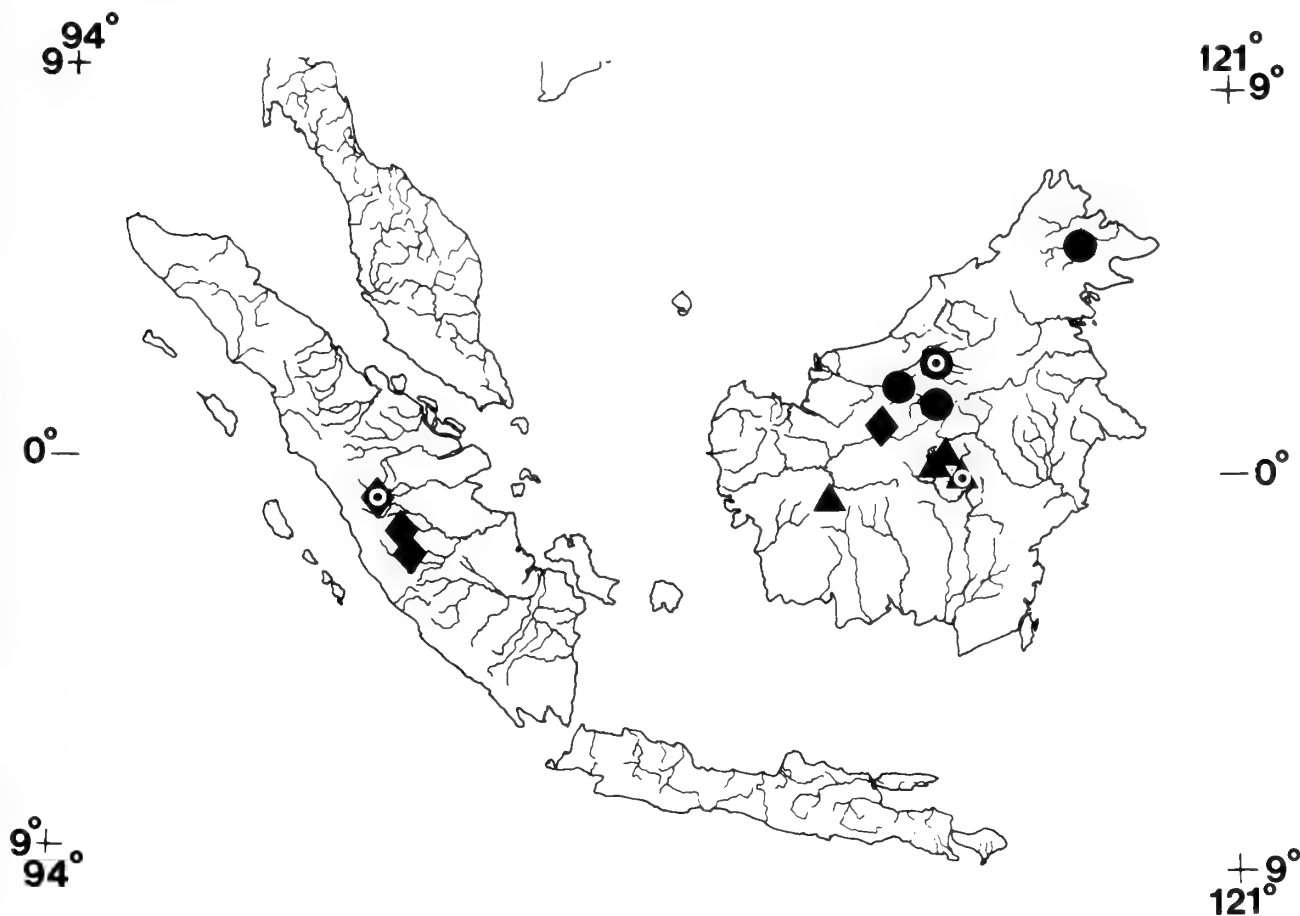


Fig. 5 Localities from which *Schismatorhynchus* material was examined in this study; \blacklozenge = *S. heterorhynchus*, \blacktriangle = *S. endecarhapis*, and \bullet = *S. holorhynchus*; target symbols = type localities.

REMARKS. Sumatra materials appear to have a more rounded head, deeper body, and longer fins than specimens from Borneo. We attribute this to larger size of the Sumatra specimens studied, but further materials in the appropriate size range (smaller specimens from Sumatra and larger specimens from Borneo) may reveal the two populations to be different species. If so, a new name will be required for the Kapuas River species.

***Schismatorhynchus holorhynchus* sp. nov.** (Figs 1B,3,5,6)

Schismatorhynchus heterorhynchus; Inger & Chin, 1962: 86

HOLOTYPE. USNM 325389 (101.7 mm SL); Malaysia; Sarawak; confluence of Batang Balui and Batang Kerumo; 02°22'N 113°45'E; col. L. Parenti, K. Luhut, and A. Among; 3-VIII-1991; field no. LRP 91-28.

PARATYPES. USNM 346637 (12 including 1 cleared and counter stained, 39.5–78.8 mm SL); data as for holotype.

NON-TYPE MATERIALS. Borneo (Kinabatangan River basin, Sabah, Malaysia) – FMNH 68548 (28, 28.3–34.8 mm SL); small stream 1 mi. above Sungei Tabalin Besar, Sta. 1; col. R. Inger and P.K. Chin; 21 April 1956. FMNH 68549 (1, 49.3 mm SL); Deramakot Camp, hill

stream; col. R. Inger; 2 May 1956. FMNH 68550 (5, 42.7–79.3 mm SL); Deramakot Camp, hill stream below waterfall; col. R. Inger and P.K. Chin; 2 May 1956. FMNH 68551 (1, 47.8 mm SL); Deramakot Camp, stream below water fall; col. R. Inger; 3 May 1956. FMNH 68552 (30 of 147, 30.3–49.4 mm SL); Deramakot Camp; col. R. Inger and P.K. Chin; 8 May 1956. FMNH 94183 (1, 55.8 mm SL); Deramakot Camp, hill stream; col. R. Inger; 2 May 1956.

Borneo (Rejang River basin, Sarawak, Malaysia) – USNM 325359 (2, 21.8–55.8 mm SL); Baleh River, creek entering northern bank approx 5 km E of Sut River; 2°2'N 113°07'E; col. L. Parenti *et al.*; 25 Jul 1991. USNM 324978 (2, 33.5–35.5 mm SL); Baleh River, stream entering river opposite Sekolah Negara Bawai; 2°0'N 113°03'E; col. L. Parenti *et al.*; 24 Jul 1991. USNM 325387 (2, 59.2–59.5 mm SL); Baleh River, creek entering southern bank approx. 20 km E of Sut River; 2°01'N 113°06'E; col. L. Parenti *et al.*; 24 Jul 1991. USNM 325388 (2, 67.6–68.7 mm SL); Batang Balui, Batang Tamn were it enters Bantan Balui; 02°22'N 113°47'E; col. L. Parenti *et al.*; 6 Aug 1991. USNM 325390 (18, 36.2–77.2); Batang Balui, Batang Lut at Batang Balui; 2°22'N 113°46'E; col. L. Parenti *et al.*; 3 Aug 1991. USNM 325411 (28, 38.7–77.6 mm SL); Batang Balui, stream near mouth; 2°20'N 113°49'E; L. Parenti *et al.*; 6 Aug 1991.

DIAGNOSIS. A species of *Schismatorhynchus* with eight branched

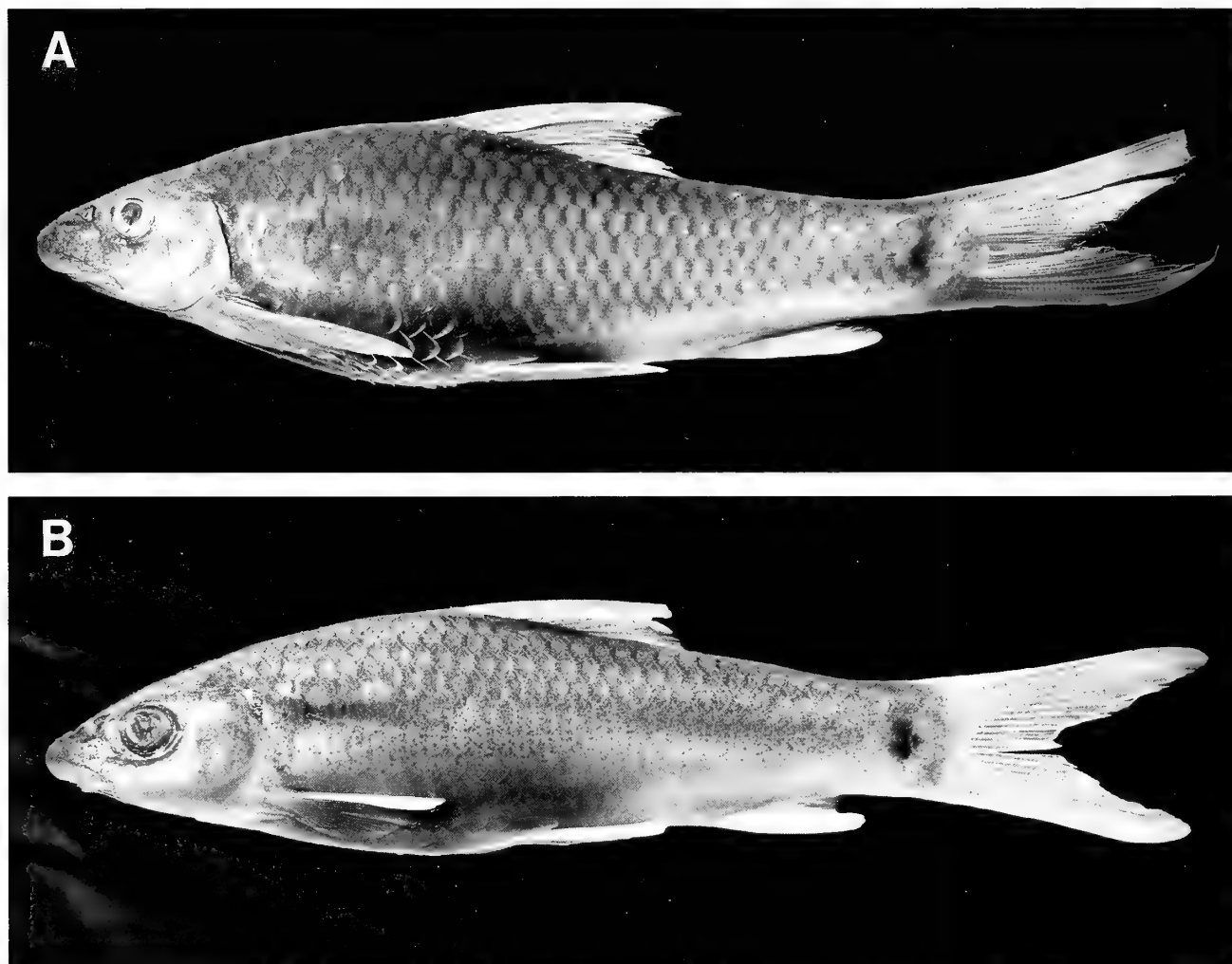


Fig. 6 Photographs of the holotype (A. USNM 325389, 101.7 mm SL) and a small (B. USNM 325890, 43.6 mm SL) specimen of *S. holorhynchus*.

Table 3 Vertebrae, branched rays in dorsal fin, and pairs of pleural ribs counts for species of *Schismatorhynchus*; the mean is followed (\pm) by the standard deviation; the range is reported as the minimum and maximum observations; sample size is reported in the column heading.

	<i>S. heterorhynchus</i> n=38	<i>S. holorhynchus</i> n=99	<i>S. endecarhapis</i> n=45
Vertebrae	31 \pm 0.0	32.0 \pm 0.10 31–32	33.0 \pm 0.15 32–33
Precaudal vertebrae	15.9 \pm 0.23 15–16	16.0 \pm 0.17 15–16	16.9 \pm 0.32 16–17
Caudal vertebrae	15.1 \pm 0.23 15–16	16.0 \pm 0.14 16–17	16.1 \pm 0.36 15–17
Peduncular vertebrae	5.4 \pm 0.50 5–6	5.8 \pm 0.48 5–7	5.8 \pm 0.44 5–6
Dorsal fin position	8.0 \pm 0.23 7–9	7.9 \pm 0.30 7–8	8.0 \pm 0.0
Anal fin position	18.9 \pm 0.23 18–19	19.0 \pm 0.46 19–20	20.1 \pm 0.32 20–21
Branched dorsal-fin rays	8 \pm 0.0	8.0 \pm 0.10 7–8	11.0 \pm 0.40 10–12
Ribs	12.3 \pm 0.47 12–13	10.3 \pm 0.51 9–11	12.7 \pm 0.45 12–13

rays in dorsal fin (*S. endecarhapis* with 11 branched rays in dorsal fin); snout pointed, without cleft (*S. heterorhynchus* with deep cleft in snout), tuberculate, tubercles conical, becoming multicuspoid to stellate in individuals about 60 mm SL and greater (*S. heterorhynchus* with pyramidal tubercles; *S. endecarhapis* with simple, conical tubercles); a round blotch on caudal peduncle (*S. heterorhynchus* and *S. endecarhapis* without round blotch on caudal peduncle).

DESCRIPTION. The largest specimen available for study is about 102 mm SL, however the species grows considerably larger in Sungai Sebangu (K.Martin-Smith, pers. comm.) The overall form of the body is shown in Figure 6. Selected morphometric ratios, meristic information, and vertebral counts are reported in Tables 1–3.

Snout pointed, tuberculate, tubercles moderate in size, absent from region of the cleft in snout of *S. heterorhynchus*. Two pairs of barbels, anterior pair small and fitting in groove, posterior pair hidden in deep recess at mouth corner.

Mouth C-shaped, usually distinctly wider than long (mean Mw:MI = 1.8, range 1.3–2.2, SE 0.07, n=10). Cutting edge of lower jaw emergent, its tips extend posteriorly to vertical line from anterior margin of pupil. Lateral lobe of lower lip thick.

Snout and dorsal surface of head posterior to nares and body anterior to dorsal fin tuberculate. Snout heavily tuberculate. Tubercles in region of snout well-developed, conical, multicuspoidate in larger specimens (Fig. 3B) but simple in specimens less than about 60 mm SL. Rostral tubercles present laterally on first infraorbital (Io 1), around tip of snout, over dorsal surface of tip of snout, between nares, and between nares and eye. Tubercles absent from a patch between front edge of ethmoid and anterior part of snout that corresponds in position to the deep cleft in snout of *S. heterorhynchus* (Inger and Chin, 1962). Region between dorsal fin and nares covered by numerous fine tubercles.

Dorsal fin origin in advance of pelvic fin, margin slightly convex. Pelvic fin origin at 3rd branched ray of dorsal fin. Pectoral fin less than head length. Caudal fin forked.

Lateral line complete, slightly curved, running in the middle of caudal peduncle posteriorly, usually with 31 scales to end of hypural plate (Table 2), 5½ scales above lateral line to dorsal origin; 4½ scales below lateral line. Vertebrae usually 32, usually with 16 precaudal and caudal vertebrae. Number pairs of pleural ribs usually 10 or 11.

In alcohol dark from above, creamy below. Indistinct, dark, lateral band present, its origin before origin of dorsal fin. Band width equivalent to width of one scale row, anteriorly lateral band lies above lateral line, posteriorly lateral band lies over lateral line. Precaudal spot present, very distinct in small individuals, larger but may be obscure in larger individuals. Side of body above middle of pectoral fin with a few scales darkly marked.

ETYMOLOGY. The name *holorhynchus* is from the Greek words *holos*, meaning whole or entire, and *rhynchus*, meaning snout. It is

in reference to the new species' snout, which lacks the deep cleft found in the snout of its sister species, *S. heterorhynchus*.

DISTRIBUTION. Materials of *S. holorhynchus* originate from within the Rejang River basin, Sarawak, Malaysia and the Kinabatangan River basin, Sabah (North Borneo), Malaysia (Fig. 5). The species has also been collected to the south of the Kinabatangan River, in the Segama River basin in Sabah (K.Martin-Smith pers. com.). The Sarawak and Sabah localities from which *S. holorhynchus* has been taken are distant from one another and the Rejang and Kinabatangan rivers which it is known to inhabit flow off Borneo in different directions and into different seas. It would be remarkable if *S. holorhynchus* was discovered not to inhabit some of the many river basins lying between the two rivers from which it has been collected.

Schismatorhynchus endecarhapis sp. nov. (Figs 1C, 3, 5, 7)

Schismatorhynchus heterorhynchus; Roberts, 1989: 79, Fig. 58.

HOLOTYPE. MZB 6092 (179.0 mm SL); Indonesia; Kalimantan Tengah; Barito River drainage; Sungai Laung at Desa Maruwei (0°21.986'S 114°44.103'E); hook and line; col. D.J. Siebert, A.H. Tjakrawidjaja and O. Crimmen; 15–18 Jul 1992; field no. DS-12-1992.

PARATYPES. BMNH 1993.5.12:1–19 (19, 61.9–41.8 mm S); Indonesia; Kalimantan Tengah; Barito River basin; mouth of small stream at Project Barito Ulu base camp on Sungai Busang; seine; col. D.J. Siebert, A.H. Tjakrawidjaja and O. Crimmen; 27–28 Jan 1991; field no. 3-DJS-1991. MZB 3434 (1, 88 mm SL); Indonesia; Kalimantan Barat; Kapuas River basin; rocky channel in mainstream of Sungai Pinoh at Naga Saian, 45 km S of Nagapinoh; 0°43'S 111°38.5'E; rotenone; col. T.R. Roberts and S. Wirjoatmodjo; 26 Jul 1976; field no. Kapuas 1976-29.

NON-TYPE MATERIALS. Borneo (Barito River basin, Kalimantan Tengah, Indonesia) – BMNH 1993.5.12:52–61 (10, 43.3–22.3 mm SL); sand bars of Sungai Joloi above its confluence with Sungai Busang; seine; col. D.J. Siebert, A.H. Tjakrawidjaja and O. Crimmen; 8 Feb 1991; field no. 13-DJS-1991. BMNH 1993.5.12:62–74 (13, 48.0–26.5 mm SL); sand bars of Sungai Murung around Project Barito Ulu base camp on Murung River; seine; col. D.J. Siebert, A.H. Tjakrawidjaja and O. Crimmen; 12 Feb 1991; field no. 16-DJS-1991. BMNH 1993.5.31–51 (21, 48.2–19.4 mm SL); Barito River at Desa Muara Laung; 0°34.576'S 114°44.205'E; seine; D.J. Siebert, A.H. Tjakrawidjaja and O. Crimmen; 20–22 Feb 1991; field no. 22-DJS-1991. BMNH 1993.5.12:20–30 (11, 46.7–34.4 mm S); sand bars of Sungai Busang at Project Barito Ulu base camp on Sungai Busang; seine; D.J. Siebert, A.H. Tjakrawidjaja, O. Crimmen; 14–15 Feb 1991; field no. 18-DJS-1991.

Borneo (Kapuas River basin, Kalimantan Barat, Indonesia) – MZB 3434 (1, 88 mm SL); Sungai Pinoh at Naga Saian; 0°43'S

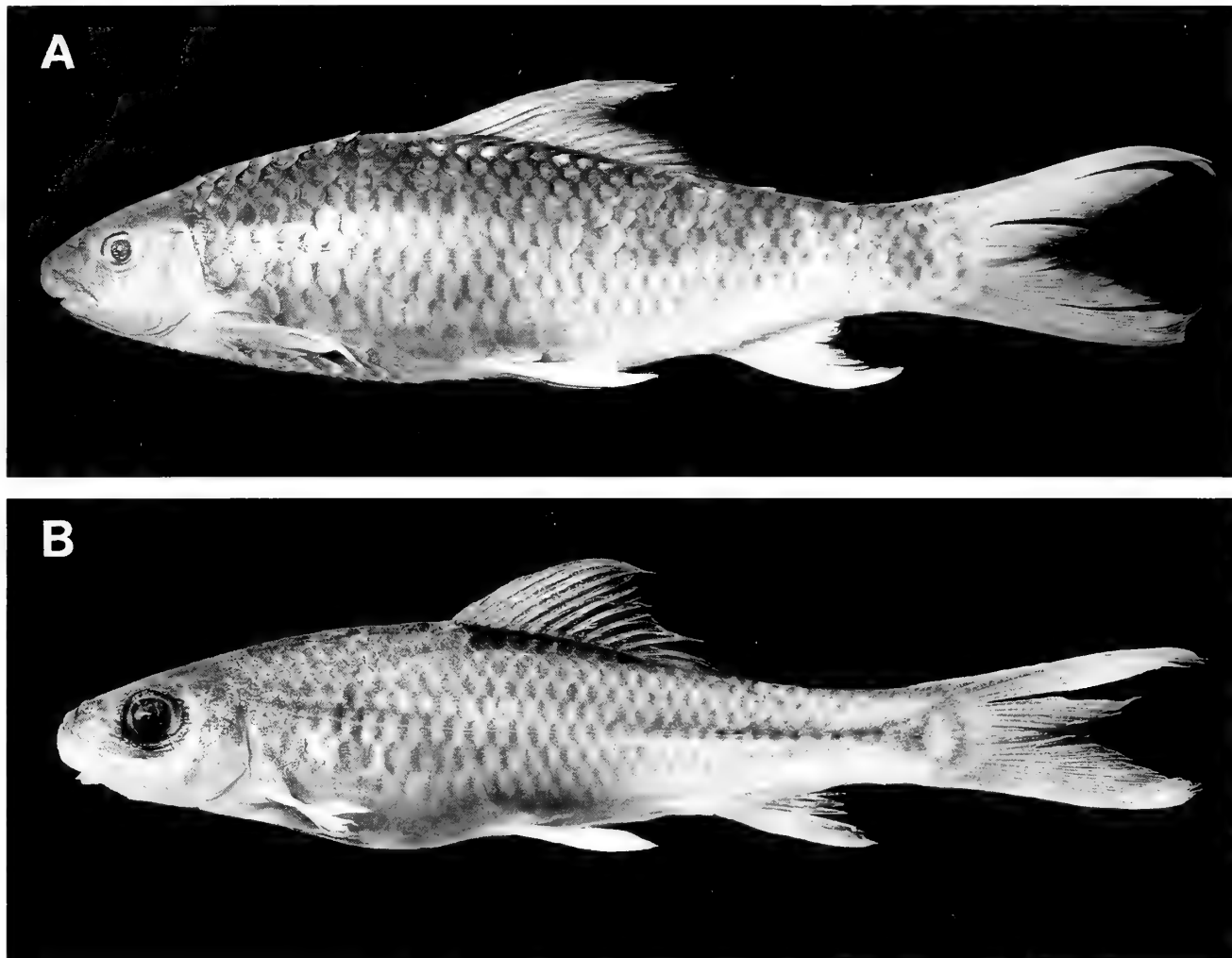


Fig. 7 *Schismatorhynchos endecarhapis*: A. MZB 6092, holotype, 179.0 mm SL; B. *S. endecarhapis*, BMNH 1993.5.12:1–19, paratype, juvenile, 59.4 mm SL.

111°38.5'E; rotenone; T.R. Roberts; 26 July 1976; field no. Kapuas 1976-29. MZB 3433 (2); Sungai Pinoh 37 km S of Nagapinoh; 0°39.5'S 111°40'E; rotenone; T.R. Roberts; 24 July 1976; field no. Kapuas 1976-27.

DIAGNOSIS. A species of *Schismatorhynchos* with 11 branched rays in dorsal fin (*S. heterorhynchos* and *S. holorhynchos* with eight branched rays in dorsal fin); snout entire (*S. heterorhynchos* with cleft snout); tubercles conical, simple (*S. heterorhynchos* with pyramidal tubercles, *S. holorhynchos* with multicuspid tubercles); gape not reaching vertical from anterior margin of eye (*S. heterorhynchos* and *S. holorhynchos* with gape reaching to beyond anterior margin of eye); modally 33 pored lateral line scales (*S. heterorhynchos* usually with 31–32 pored lateral line scales, *S. holorhynchos* usually with 31 pored lateral line scales).

DESCRIPTION. Material available for study consists of small specimens and one larger individual (holotype). The gap in size between the largest of the smaller material and the holotype is so large that study of allometry and shape change with size is not feasible. The overall form of *Schismatorhynchos endecarhapis* is shown in Figure 7. Selected meristic, morphometric, and vertebral data are presented in Tables 1–3.

Head length moderate (Table 1); gape reaching to a little before anterior margin of eye; snout with well developed rostral cap. Two pairs of barbels, anterior barbel in groove on snout, shorter than posterior barbel; posterior barbel about equal to eye diameter.

Mouth crescentic, more than twice as wide as long (mean $Mw:MI = 2.4$; range 2.2–2.8; SE 0.08; $n=9$). Upper lip well separated from rostral cap, not continuous with lower lip around corner of mouth. Lower jaw with a sharp horny covering. Median lobe of lower lip wide, covering most of lower jaw, continuous with isthmus, separated from well developed lateral lobes of lower lip by a deep postlabial groove.

Only a single large specimen of this species is known; observations of the extent of tuberculation are thus limited in scope. Small individuals with a few small tubercles, large individual with many small tubercles. Snout tuberculate, a small patch of large, unicuspid, conical tubercles present just above and before rostral barbel (Fig. 3C). Smaller tubercles present around anterior face of rostral cap. No large tubercles on Io 1 nor in space between nares and eyes. Fine tubercles present over dorsal surface of head but appear to be absent between nape and dorsal fin.

Dorsal fin long, with 11 branched fin-rays (1 individual with 10, 1 individual with 12), origin well in advance of pelvic fins. Margin

of dorsal fin falciform, first few anterior principal rays long. Caudal fin forked.

Lateral line nearly straight, with 33 scales to end of hypural plate; $5\frac{1}{2}$ scales above lateral line to dorsal origin; $4\frac{1}{2}$ scales below lateral line. Vertebrae usually 33 (2 of 35 individuals with 32), usually with 17 precaudal vertebrae and 16 caudal vertebrae. Number of pairs of pleural ribs usually 13.

Colour in alcohol dark above, lighter below (Fig. 7). Scale pockets of scale rows to at least 2 scale rows below lateral line with a distinct, dark crescent. A dark lateral stripe evident, terminating in a distinctly triangular precaudal spot. In larger individuals stripe consists of coloration centred over 3 scale rows; stripe on lateral line scale row begins below posterior end of dorsal fin, on 1st scale row above lateral line stripe begins at dorsal origin and ends at precaudal spot, on 2nd scale row above lateral line stripe begins midway between occiput and dorsal origin and ends midway along peduncle; in small individuals stripe evident on lateral line scale row only. Small individuals with a prominent mark on side at 5th or 6th scale along lateral line (Fig. 1b), usually a scale above and below lateral line darkened along with 1 or 2 scales on lateral line. Dorsal and caudal fins dusky, interradial membranes heavily marked with melanophores. Interradial membranes of pectoral and pelvic fins lightly marked with melanophores.

ETYMOLOGY. The species name *endecarhapis* is formed from the Greek words *endeka* (eleven) and *rhapis* (rod), referring to the modal number (11) of branched rays in dorsal fin. It is proposed as a noun in apposition.

DISTRIBUTION. *Schismatorhynchus endecarhapis* is known from the Barito River above Muara Teweh and from Sungai Pinoh of the Kapuas River system (Fig. 5). Whether or not the species occurs in the lower reaches of these watersheds where streams are larger is not yet known. In the Barito small individuals were seined at creek mouths and on sand bars along the mainstream.

REMARKS. The largest individual was taken by hook and line, baited with beetle larvae, below floating houses at Desa Maruwei, indicating that the species is an opportunistic feeder even though the length of its intestine would indicate it is predominately a herbivore.

Intragenetic comparisons

Species of *Schismatorhynchus* are easily distinguished from one another and gross differences are employed in the key to species. The meristic information of Table 3 is summarised graphically in Figure 8. Axis 1, which can be interpreted as an axis of dorsal fin branched ray and caudal vertebrae counts, provides a dimension along which *S. endecarhapis* is clearly separable from *S. heterorhynchus* and *S. holorhynchus*. Axis 2, interpreted as an axis of overall vertebral pattern and rib count, separates *S. heterorhynchus* and *S. holorhynchus*. Figure 9 summarises the morphometric information of Table 1. Complete separation of the three species is achieved in the two dimensions of Axis 1 and Axis 2. Axis 1 is interpreted as a head length/dorsal-fin base length axis. Axis 2 is a contrast of dorsal-fin base length and caudal peduncle depth.

TUBERCULATION PATTERNS. Species specific tubercle distribution patterns in *Schismatorhynchus* are evident at small size. The regions of the snout which will eventually contain large tubercles are apparent at sizes smaller than 30 mm SL in *S. endecarhapis*, and *S. holorhynchus*, well before the tubercles undergo obvious enlargement.

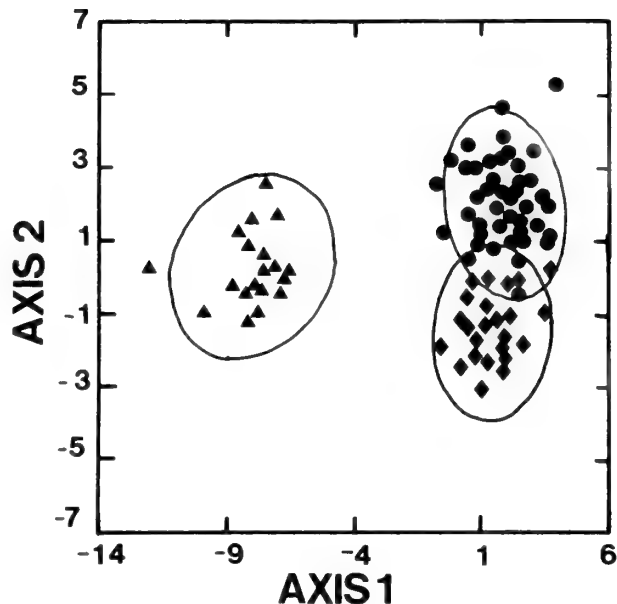


Fig. 8 Graphical joint summary of the meristic information for species of *Schismatorhynchus* with 0.95 confidence ellipses of samples (*S. heterorhynchus* = ♦; *S. holorhynchus* = ●; *S. endecarhapis* = ▲). Standardised discriminant function for: Axis 1 = $0.03 \times \text{anal fin position} + 0.26 \times \text{peduncular vertebrae count} - 1.68 \times \text{caudal vertebrae count} - 1.49 \times \text{precaudal vertebrae count} - 0.09 \times \text{rib count} - 0.04 \times \text{dorsal fin position} - 0.75 \times \text{number of branched rays in dorsal fin}$; Axis 2 = $0.01 \times \text{anal fin position} + 1.32 \times \text{caudal vertebrae count} + 0.05 \times \text{peduncular vertebrae count} + 1.23 \times \text{precaudal vertebrae count} - 0.57 \times \text{rib count} - 0.03 \times \text{dorsal fin position} - 0.49 \times \text{number of branched rays in dorsal fin}$; Wilk's lambda = 0.001, df 7,2,173, $p < 0.0001$.

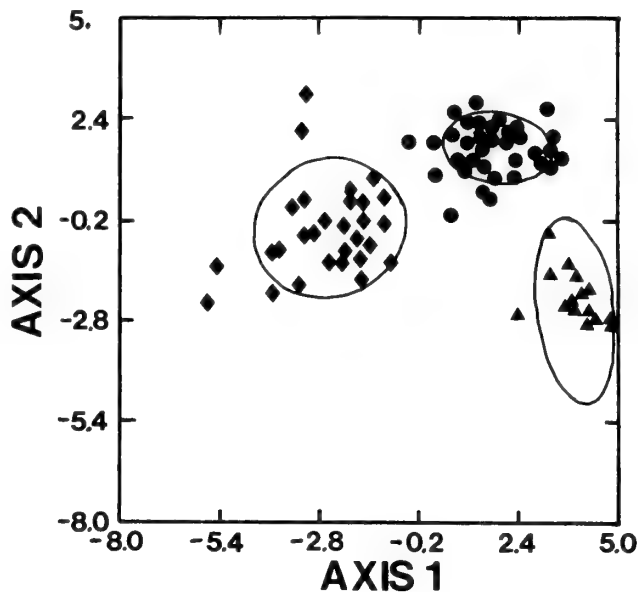


Fig. 9 Graphical joint summary of the selected morphometrics of species of *Schismatorhynchus* with 0.75 confidence ellipses of samples (*S. heterorhynchus* = ♦; *S. holorhynchus* = ●; *S. endecarhapis* = ▲). Standardised discriminant function for: Axis 1 = $2.39 \times \text{body depth} + 2.01 \times \text{dorsal base} + 1.55 \times \text{predorsal length} - 1.21 \times \text{caudal peduncle depth} - 0.49 \times \text{eye length} - 3.77 \times \text{head length} - 0.88 \times \text{snout length}$; Axis 2 = $0.98 \times \text{body depth} + 4.90 \times \text{caudal peduncle depth} + 0.85 \times \text{eye length} + 0.74 \times \text{predorsal length} - 5.28 \times \text{dorsal base} - 1.40 \times \text{head length} - 0.91 \times \text{snout length}$; Wilk's lambda = 0.04, df 7,2,229, $p < 0.0001$.

DISCUSSION

Including *Schismatorhynchos endecarhapis* and *S. holorrhynchos* in the genus *Schismatorhynchos* raises a number of theoretical and practical problems, as would including them in the obvious alternative, *Lobocheilos*. Bleeker's (1863) diagnosis of *Schismatorhynchos* includes, among other things, mention of a deep, transverse cleft of the snout and the upper and lower lips not continuous around the corner of the mouth. Weber & de Beaufort (1916; Fig. 86) described an additional oro-labial structure of *Schismatorhynchos*, a frenulum between the lateral lobe of the lower lip and the isthmus (Fig. 2A). Hindsight shows that the cleft snout is characteristic, so far as is known, of a single species (*S. heterorrhynchos*) while the oro-labial features are found in at least two additional species. Our decision to include the new species in *Schismatorhynchos* rests on these oro-labial features, which we consider derived for Southeast Asian labeonins (we recognise them as synapomorphies of the genus *Schismatorhynchos*).

The problem, and it is nothing more than that of including additional species in any monotypic genus with a very specific, highly descriptive name, of including the two new species in *Schismatorhynchos* is that both lack a cleft in the snout. However, the problem is not so much that the two new species lack a cleft snout but that the highly descriptive generic name *Schismatorhynchos* is apt for only one species of the genus. Generic names serve two functions in modern classification: 1) the first element of a unique binomen; and 2) the name of a group of species that are close phylogenetic relatives of each other. The first function is a matter of nomenclature. The second function lies within the realm of the science of Systematics and we believe it to be of greater importance. Since there is good evidence (the oro-labial features) that the two new species are close relatives of *S. heterorrhynchos* we include them in *Schismatorhynchos* even though they lack a cleft snout. This leaves the name *Schismatorhynchos* apt for only one of the three species in the genus but we do not see this as reason enough to propose a new generic name for the other two, especially since *S. holorrhynchos* is probably more closely related to *S. heterorrhynchos* than it is to *S. endecarhapis*.

Lobocheilos is herein recognised as that group of Southeast Asian cyprinids possessing a very wide median lobe of the lower lip and with the lower and upper lips continuous around the corner of the mouth (Fig. 1D). This definition conforms to that of Smith (1945), who followed de Beaufort's (1927) comment on an Indo-Australian subgroup of *Tylognathus* Heckel. The two new species of *Schismatorhynchos* could have been assigned to *Lobocheilos*, as lip structure (generally) and scale and vertebral counts of the new species of *Schismatorhynchos* do conform to those of species of *Lobocheilos*. Some may prefer such an assignment, especially since the new species lack a rostral cleft, but to do so on the basis of the absence of a rostral cleft ignores the two derived oro-labial characters which all species of *Schismatorhynchos* share. As we pointed out above, we choose to focus on the evidence that the two new species are closely related to *S. heterorrhynchos* rather than their lack of a cleft in the snout.

A more practical problem is that *Schismatorhynchos endecarhapis* will not key to genus using any regional key in general use of which we are aware (Weber and de Beaufort, 1916; Smith, 1945; Inger and Chin, 1962; Kottelat *et al.*, 1993). The initial problem encountered in these keys is the count of branched rays in the dorsal fin. *Schismatorhynchos heterorrhynchos* Bleeker, *S. holorrhynchos*, and members of the closely related genus *Lobocheilos* possess fewer than 10, usually only eight, branched

rays in the dorsal fin. *Schismatorhynchos endecarhapis*, with 11 branched rays in the dorsal fin, fails this distinction, instead falling into *Tylognathus*, *Labeo*, or *Cirrhinus* (depending on which key is used).

The second problem is that a deep rostral cleft is used to separate *Schismatorhynchos* and *Lobocheilos*. Both new species of *Schismatorhynchos* fail this distinction. However, to our knowledge, the characters of upper and lower lips not continuous around the corner of the mouth and presence of a frenulum between the lower lip and the isthmus always separates *Lobocheilos* and *Schismatorhynchos* correctly.

Annotations to keys to cyprinid genera of the region.

We suggest the following annotation to the Cyprininae key of Weber & de Beaufort (1916; p. 94):

1. Suborbital bone covering greatest part of cheek; lower jaw with symphyseal tubercle; the broadly reflected lower lip not separated from jaw *Barbichthys*
2. Ring of suborbital bones not enlarged, lower jaw without symphyseal tubercle; lower lip distinct from lower jaw.
 - a. lower and upper lips not continuous around the corner of the jaw *Schismatorhynchos*
 - b. lower and upper lips continuous around corner of lower jaw.
 - aa. Dorsal with 10–18 branched rays *Labeo*
 - bb. Dorsal with 8–9 branched rays *Lobocheilos*

The key to genera of Cyprinidae of Kottelat, *et al* (1993; p. 29) can accommodate an expanded *Schismatorhynchos* with the following modifications (which make couplet 30 unnecessary).

- 27a. Suborbital bones enlarged and covering most of cheek (Fig. 109); lower jaw with a symphyseal knob; lower lip reflected backwards, but not separated from jaw *Barbichthys*
- 27b. Suborbital bones not enlarged; no symphyseal knob on lower jaw; lower lip distinctly separated from lower jaw go to *
 - *a. lower and upper lips not continuous around corner of lower jaw *Schismatorhynchos*
 - *b. lower and upper lips continuous around corner of lower jaw go to 28
 - 28a. 10–18 ½ branched dorsal rays go to 29
 - 28b. 8–9 ½ branched dorsal rays *Lobocheilos*

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CONTENTS

- 1 **A revision of the cladoceran genus *Simocephalus* (Crustacea, Daphniidae)**
Marina J. Orlova-Bienkowskaja
- 63 **Structural niche, limb morphology and locomotion in lacertid lizards (Squamata, Lacertidae); a preliminary survey**
E.N. Arnold
- 91 ***Heteroleotris georgegilli*, a new species of gobiid fish, with notes on other Mauritian *Heteroleotris* species**
Anthony C. Gill
- 97 **Revision of *Schismatorhynchus* Bleeker, 1855 (Teleostei, Cyprinidae), with the description of two new species from Borneo**
Darrell J. Siebert and Agus H. Tjakrawidjaja